Universidade de Aveiro Departamento de Biologia

Ano 2018

ÁNGELA LLAVONA VALLINA

PARÂMETROS POPULACIONAIS E ESTRUTURA GENÉTICA DO BÔTO (*PHOCOENA PHOCOENA*, L. 1758) NA COSTA NOROESTE DA PENÍNSULA IBÉRICA

POPULATION PARAMETERS AND GENETIC STRUCTURE OF THE HARBOUR PORPOISE (*PHOCOENA PHOCOENA,* L. 1758) IN THE NORTHWEST THE IBERIAN PENINSULA

Universidade de Aveiro

Departamento de Biologia

Ano 2018

ÁNGELA LLAVONA VALLINA

POPULATION PARAMETERS AND GENETIC STRUCTURE OF THE HARBOUR PORPOISE (*PHOCOENA PHOCOENA*, L. 1758) IN THE NORTHWEST IBERIAN PENINSULA

Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia.

Apoio financeiro da FCT e do FSE no âmbito do III Quadro Comunitário de Apoio.

A la mi familia,

“Canción del valor para caminar
a donde quieras llegar
mi canción del valor
y que de presa te hagas cazador”.

Igor Paskual

o júri

Presidente

Prof. Catedrático Doutor Joaquim Manuel Vieira
Professor Catedrático da Universidade de Aveiro, Portugal

Doutora Emer Rogan
Senior Lecturer da University College Cork, Irlanda

Doutor Ángel Francisco González González
Investigador Cientifico do Instituto de Investigaciones Marinas (CSIC), Espanha

Doutor Ulisses Manuel de Miranda Azeiteiro
Professor Associado com Agregação da Universidade de Aveiro, Portugal

Prof. Doutor Graham John Pierce
Investigador Sénior do Instituto de Investigaciones Marinas (CSIC), Espanha

Prof. Catedrático Doutor Amadeu Mortágua Velho da Maia Soares
Professor Catedrático da Universidade de Aveiro, Portugal

agradecimentos

It took me a lot of time and effort to carry out this PhD project, but too many people was there to make it easier.

First of all, I would like to thank my supervisors who made this work possible. Grazas Alfredo López pela idea de facer este traballo e axudarme a poder levalo a cabo, grazas polo debuxo da toniña (non podía faltar esta palabra nesta tese), grazas pola túa forma de ver a natureza e a conservación. Graças a José V. Vingada por deixar-me unir o trabalho que levamos a cabo em Galiza com o de Portugal, obrigada por me ajudar a encontrar a forma de realizar este projeto. Thank you very much to Graham J. Pierce to show me how to analyse the data, to do scientific writing and correct my English!, thank you for your patience with my questions, thank you very much for been always available.

Although not an official supervisor, Stuart B. Piertney was very close to be one. Thank you very much for receiving me in your laboratory at University of Aberdeen, thank you for show me conservation genetics, thank you for your patience with me and my “I don’t have time to do all this work” and let me be part of your team.

Because to carry out the genetic work lots of samples were needed, I would like to thank all the people and Institutions that thought that this project was worth of their collaboration: Willy Dabin (Université de La Rochelle-CNRS), Rob Deaville (Zoological Society of London), Thierry Jauniaux (University of Liege), Emer Rogan (University College Cork), Arda M. Tonay and Ayhan Dede (Istanbul University, Turkish Marine Research Foundation), Andrew Brownlow (Scottish Marine Animal Stranding Scheme), Luis Laria (CEPESMA), Carolina Fernández (Junta de Andalucía), Pablo Cermeño (AMBAR), and of course, CEMMA and SPVS.

Also I would like to thank Vasilis D. Valavanis (Helenic Center of Marine Reseach) for provindig me the environmental data needed for the habitat modelling, thank you also for answer my questions so fast.

Finally, thank you very much to Prof. Catedrático Doutor Amadeu Mortágua Velho da Maia Soares, without your help, this work would never see the light.

The study of cetaceans means ages of hours of observation, of living in small places such as boats, of spending a lot of time in the car, of time through sunny, windy, rainy, cold days, of long walks along beaches searching stranding animals, endless days from stranding to stranding, which can become great moments if you spend them with great people such as the ones I had the luck to meet…Pablo Covelo, Jose M. Cedeira, Juan Ignacio Díaz, Yosy Cartelle, Gonzálo Palacios, Begoña de la Torre, Paula Pérez, Luz Santos, Juan José Dios (JuanIlla), Ruth Fernández, Vanessa Bracali, Mara Caldas, Xesús Morales, Xulio Valeiras, Esther Abad, Josep M. Alonso, María Llarena (¡¡agracias por tu ayuda con los trámites!!), Tito Salvadores, y moitos máis voluntarios da CEMMA. ¡Grazas a tod@!

Gracias á CEMMA por deixarme usar súas fotos (portada principal, portada capítulo I, III, IV, V). Gracias también a Urki por su preciosa foto (portada capítulo VI). Eeskerrik asko.

Também quero agradecer a todos os voluntaries dá SPVS, especialmente a Marisa Ferreira, Silvia Monteiro, Jorge Santos, Helder Araújo, Isabel Oliveira e Ana Marçalo. Obrigada!

Some of them had become to be very important people in my life.

Gracias Pablo por los buenos momentos, las risas, tu apoyo y ayuda en todo momento. Gracias por mandarme los papers “por si se me pasaba”. ¡Moitas gracias!

Gracias a Mara por nuestros largos paseos bajo el sol y la lluvia arreglando el mundo. ¡Besos a Pepe!

Gracias a Vane por hacerme reír incluso haciendo cosas tan aburridas como meter datos en el excel (esas becarias!!). ¡Grazie mille!

Obrigada Silvia por as nossas charlas “desestresantes” e as visitas surpresa.

Obrigada Marisa por compartilhar as suas descobertas com grande entusiasmo.

¡Las dos siempre seréis bienvenidas de nuevo en mi casa!

Although the beginning of my stay in Aberdeen was hard, I have very good memories of the time spent there. Thanks again Stuart, you were not only a good “supervisor” (Master Jedi), but also a good friend. Thank you to all his team, especially to Heather Ritchie (you were right, at the end, I was ok), Martha Gavan and Marius Wezel. You’re cool guys! Thank you for your help and make me laugh!

I’m also thankful to Gillian Murray-Dickson. Thank you for your help, your borrowed place and for introduce me Sol and Simon. It was great to live with you two, spend time crocheting with Sol, listen to Simon’s music, and watch films together.

Thanks to my “Spanish” family in Aberdeen: Ana Castañé, Pablo, Miriam, Nacho, Ana Amorim, Susana, y muy especialmente a Yolanda (¡nena, menos mal que nos teníamos la una a la otra!).

Hay tres personas a las que quiero agradecer haber estado ahí a lo largo de los años, ¡casi siglos!, aunque no nos viéramos mucho en algunas épocas: Lucía, Isa y Paula. Especialmente a Lucía, que desde que volvió a Asturies ha hecho que mi tiempo libre sea “más y mejor”, gracies por presentarme a gente tan genial como Tarkil, Keven, Almu, Luis, Sonia, Tika y Rosa. Gracias Lu y Tark por dejarme cuidar de Elia, siempre me saca una sonrisa. (Ahora tendré más tiempo para preparar mis personajes, ¡oh, Tarkil, mi gran Master del Universo!).

Hay otra persona que, al igual que Pablo, ha estado siempre ahí desde que llegué a Vigo. Gracias a Iria por su (escasa) paciencia (que conmigo es mucha), gracias por escucharme y entenderme, gracias por apoyarme y animarme, gracias por tus comentarios malvados y sarcásticos (¡qué risas!). Bananaaaaaaaa.

Por último, tengo muchísimo que agradecer a mi familia, que han estado apoyándome toda mi vida y han tenido la paciencia de soportarme en momentos de agobio a los que hacer una tesis siempre te lleva. Sin vosotros no habría llegado hasta aquí, ¡¡muches gracies!!

palavras-chave

Boto, Phocoena phocoena, genética, ADN, microsatélites, ADN mitocondrial, distribuição, modelação de habitat, GAM, monitorizações de barco, monitorizações costeiras, arrojamentos.

resumo

O principal objectivo desta tese consistiu em fornecer informação sobre boto (*Phocoena phocoena*) no Nordeste da Península Ibérica (NOPI), uma vez que esta espécie é designada como "Vulnerável" em Espanha e Portugal (Catálogo Nacional de Especies Amenazadas, Lei 4/1989, 2000; Livro vermelho dos vertebrados de Portugal) e está incluida no Anexo II da Directiva Habitats, requerendo assim a designação de Áreas Especiais de Conservação (AEC) pelos estados membros da UE. O estudo das populações desta espécie é uma prioridade e tanto a IWC (International Whaling Commission) como a ICES (International Council for the Exploration of the Sea) recomendam a realização de estudos para determinar a sua estrutura populacional e desenvolver estratégias de gestão adequadas, de forma a reduzir os impactos negativos nas populações. Adicionalmente, o estudo da distribuição, abundância e dinâmica populacional de cetáceos são considerados em alguns membros da EU indicadores do "Bom Estado Ambiental" das águas marinhas europeias, segundo a Directiva Quadro Estratégia Marinha (DQEM).

Como a conservação requer o conhecimento da distribuição e estrutura populacional das espécies, neste estudo a estrutura populacional do boto no nordeste Atlântico e Mar Negro foi examinada utilizando dez microsatélites e a variação da região controlo do ADN mitocondrial (mtADN). A análise de microsatélites detectou três grupos genéticos principais: a Península Ibérica, o restante nordeste Atlântico e o Mar Negro. Uma rede de haplótipos mitocondriais evidenciou o isolamento das populações do Mar Egeu-Mármara e do Mar Negro. A análise de microsatélites e de mtADN não detectou diferenças genéticas entre a Galiza e Portugal, nem qualquer padrão de estrutura genética populacional ao longo da costa Ibérica. No entanto, ocorreram diferenças entre a Península Ibérica e as restantes populações analisadas. Ambos os marcadores mostraram níveis de diversidade genética mais baixos na Península Ibérica comparativamente com outras populações, excepto as populações dos mares Egeu, Mármara e Negro. Os níveis de divergência detectados não aparentam dever-se a isolamento por distância, mas antes a segregação populacional devido a condições oceanográficas, já que os afloramentos costeiros presentes no oeste Ibérico e no nordeste Africano apresentam condições adequadas para a ocorrência de boto. Assim, os dados genéticos sugerem que os animais da Península Ibérica e do oeste Africano deverão ser considerados como uma população separada.

De seguida, foram aplicadas técnicas de modelação de habitat para estudar a distribuição de boto, uma vez que representam uma ferramenta poderosa para

descrever e prever a distribuição de cetáceos e compreender os processos ecológicos que influenciam essas distribuições. Foram utilizados dois métodos para a recolha de dados de distribuição de cetáceos, pela ONG CEMMA (Coordinadora para o Estudo dos Mamíferos Mariños): 1. monitorizações dedicadas de barco, realizadas em águas costeiras Galegas, de 2003-2010; 2. monitorizações mensais em pontos costeiros localizados ao longo da costa Galega, de 2003 a 2011. Os resultados das monitorizações de barco mostraram que: i) estados do mar superiores influenciaram negativamente a detecção de botos; ii) a largura do campo de visão tem um efeito positivo; iii) a melhor velocidade de barco para monitorizar boto é aproximadamente seis nós. Verificou-se a ocorrência de variação inter-anual, com um aumento significativo de observações em 2005 e ausência de detecções em 2006. Em contraste, não se verificou a influência das variáveis mês ou profundidade na presença de boto. Diversas variáveis ambientais parecem ser importantes para explicar a presença de botos, já que: i) foram maioritariamente visto em águas de temperaturas médias; ii) à medida que a concentraçao de clorofila e a profundidade da zona eutrófica (ZE) aumentam, verifica-se um aumento na probabilidade de presença de boto; iii) verificou-se uma relação positiva entre o número de avistamentos e a ocorrência de inclinações do fundo marinho mais acentuadas e viradas a sul. Por sua vez, a análise de avistamentos costeiros mostrou que cinco variáveis parecem influenciar a capacidade de detecção de botos, pelos observadores, nomeadamente: i) a duração da observação; ii) o campo de visão, que apresentou uma relação positiva com o número de avistamentos; iii) verificou-se um decréscimo linear nos avistamentos à medida que o Beaufort aumenta; iv) botos foram avistados mais frequentemente com valores de Douglas entre 2 e 3; v) a presença de roaz (Tursiops truncatus) teve um efeito negativo na presença de botos. Verificou-se um padrão temporal durante o período de estudo, com um aumento do número de avistamentos ao longo dos anos. De igual modo, verificou-se um aumento do número de avistamentos no final do dia e em localizações mais a norte, com maior número de detecções em Lugo e A Coruña. Condições ambientais também parecem afectar a distribuição de botos, a partir de pontos costeiros: foram detectados mais animais em águas onde a profundidade da ZE era superior, onde a profundidade era mais variável, onde a inclinação do fundo marinho era superior e onde a plataforma continental era mais estreita.

Por último, foram analisados os arrojamentos de boto recolhidos pela CEMMA na Galiza, de 1990 a 2013, e pela Sociedade Portuguesa de Vida Selvagem (SPVS) em Portugal, de 2000 a 2013. Foram registados 424 arrojamentos desta espécie na área de estudo. Verificou-se a ocorrência de arrojamentos ao longo do ano, bem como diferenças inter-anuais, com um acréscimo no número de arrojamentos com o tempo. Os números mais elevados de arrojamentos ocorreram em 1998 na Galiza e em 2011 em Portugal. De igual modo, verificou-se a ocorrência de diferenças de diferenças no número de arrojamentos entre meses. Em particular, enquanto que na Galiza os arrojamentos foram mais comuns no Inverno, com um pico em Março e Abril, em Portugal o pico de arrojamentos foi detectado em Maio. Dados de ambas as áreas mostram um maior número de arrojamentos no Inverno comparativamente com o Verão. Verificou-se um aumento no número de arrojamentos de boto de norte para sul, com picos em duas regiões: a sub-area 5 e 9. No geral, o rácio sexual nos arrojamentos foi aproximadamente de 1:1, apesar de o número de fêmeas ser ligeiramente inferior em Portugal. O comprimento total dos animais variou de 81 a 202 cm, com um tamanho médio de 146.66 cm, com botos maiores em Portugal comparativamente com a Galiza e com as fêmeas maiores que os machos. No geral, 33.4% dos botos arrojados apresentaram evidências de captura acidental em artes de pesca, com uma proporção superior na costa Portuguesa (56.0%) comparativamente com a costa Galega (26.2%), o que poderá dever-se a diferenças no tipo de artes de pesca usadas em cada área.

Os resultados do presente estudo mostram evidências de ausência de estrutura

genética na população de boto no NPI e um claro isolamento desta população comparativamente com outras populações do nordeste Atlântico e Mar Negro, devido à importante influência de processos oceanográficos, como correntes e afloramento costeiro. Estes resultados suportam a recomendada definição da população de boto da Península Ibérica como uma separada unidade de gestão para a DQEM e também a definição de uma terceira sub-espécie, *Phocoena phocoena* meridionalis. Tanto os resultados de avistamentos como os de arrojamentos mostraram que esta espécie está presente na área de estudo durante todo o ano, com variações temporais (anos, meses) e espaciais (sub-áreas), sugerindo a movimentação dos animais entre áreas. Assim, i) as áreas protegidas não podem ser sazonais, uma vez que esta espécie está presente durante todo o ano; ii) a Galiza é uma das áreas importantes para boto na Península Ibérica, quando também pode ser o caso do Golfo de Cádiz, com quatro localizações a apresentar elevada ocorrência desta espécie: Punta Candieira, Vilán e Cabo Touriñán, Punta Remedios (Lira) e Faro de Corrubedo; iii) as áreas utilizadas por boto e roaz são distintas. Adicionalmente, enquanto que parte da população de roaz foi descrita como sendo residente, a população de boto não parece comportar-se de igual modo; assim, a mesma AEC não será útil para ambas espécies, a não ser que seja suficientemente grande para abranger as áreas utilizadas por ambas.

A captura acidental em artes de pesca é uma das principais ameaças para pequenos cetáceos, especialmente boto, e constitui um factor preocupante na conservação desta espécie em áreas com elevado esforço de pesca, como NIP. Foi descrita uma maior proporção de captura acidental de boto na costa Portuguesa relativamente à Galega, potencialmente devido às diferenças nas artes de pesca usadas em cada área. De qualquer forma, em ambas as áreas (Galiza e Portugal) a mortalidade devido a captura acidental é insustentável, considerando o limite de mortalidade de 1.7% definido pela ASCOBANS (1997). No entanto, captura acidental em artes de pesca não constitui a única ameaça para esta espécie e é essencial a realização de mais estudos para enriquecer o conhecimento sobre os botos na Península Ibérica e suportar a sua conservação.

keywords

Harbour porpoise, *Phocoena phocoena,* genetics, DNA microsatellite markers, mtDNA, distribution, habitat modelling, GAM, boat-based surveys, land-based surveys, strandings

abstract

The main aim of this thesis was to provide information about harbour porpoises (*Phocoena phocoena*) in the North Western Iberian peninsula (NWIP), as they are designated as ”vulnerable” in Spain (Catálogo Nacional de Especies Amenazadas, Law 4/1989, 2000; Livro vermelho dos vertebrados de Portugal) and are included in Annex-II of the EU Habitats Directive, thus requiring the designation of Special Area of Conservation (SAC) by EU Member States in areas of critical habitat. The study of their populations is a priority issue and both IWC (International Whaling Commission) and ICES (International Council for the Exploration of the Sea) recommended studies to determine the population structure and develop appropriate management in order to reduce negative impacts on the populations. Also, the distribution, abundance and population dynamics of cetaceans are considered in some EU members as indicators of Good Environmental State (GES) of the EU's marine waters under the Marine Strategy Framework Directive (MSFD).

As conservation requires an understanding of the species´ distribution and population structure, the population structure of the harbour porpoise in the North East Atlantic and Black Sea was examined using ten DNA microsatellite markers and sequence variation from the mitochondrial control region. A Structure-based analysis of microsatellite structure identified three main genetic groups: the Iberian Peninsula, the rest of Northeast Atlantic, and the Black Sea. A median joining network of mtDNA sequences highlights the isolation of the Aegean-Marmara Sea and Black Sea populations. Neither microsatellite nor mitochondrial DNA markers detected genetic differentiation between Galicia and Portugal, nor any significant pattern of population genetic structure along the Iberian coast. However there were differences between Iberia and the rest of the populations studied. Values of genetic diversity for both markers were lower in the Iberian Peninsula than in all the other populations except those in Aegean, Marmara and Black Seas. Levels of divergence clearly cannot be explained by isolation by distance but instead are likely to be associated with population separation based upon oceanographic conditions due to the presence of upwelling conditions in West Iberia and North West Africa providing suitable conditions for porpoises. Overall the genetic data suggest that the Iberian Peninsula and West Africa should be considered as a separate population.

Secondly, habitat modelling was used as it represents a potentially powerful tool for describing and predicting cetacean distributions and understanding the ecological processes determining these distributions. Two data collection methods were used by the NGO CEMMA (Coordinadora para o Estudo dos Mamíferos MAriños): 1. Targeted boat surveys were carried out in Galician coastal waters during the years 2003-2010. 2. Data from systematic monthly

surveys from a series of evenly spaced observation points along the Galician coast were collected from 2003 to 2011. Results from boat surveys showed that: i) higher sea state negatively influenced the detection of porpoises, ii) field-of-view width had a positive effect; and, iii) the best boat speed for monitoring harbour porpoises is around 6 knots. There was interannual variation with a significant increase in the number of sightings in 2005 and no detections in 2006. In contrast, no significant differences in porpoise presence were seen between months or in relation to depth. Several environmental variables were found to be important to explain the presence of porpoises: i) they were mostly seen in waters with medium temperatures; ii) as chlorophyll concentration and the depth of the eutrophic zone increase there was an increase in the probability of porpoise presence; iii) finally, there were positive relationships between number of sightings and both steeper seabed slope and its facing to the South. The analysis of coastal observations showed that five variables had some influence on the observers in relation to the detection of porpoises. i) the duration of the observation; and, ii) the field of view had positive relationships with sightings; iii) there was a linear decrease in sightings as the Beaufort value increases; iv) porpoises were most frequently seen when Douglas values were in the range 2 to 3, and v) the presence of bottlenose dolphins (*Turisops truncatus*) had a negative effect on porpoise presence. There was a temporal trend during the study period, with an increase in the number of sightings over the years. Also, there was an increase in the number of sightings later in the day, and the number of sightings increased northwards with more detections in Lugo and A Coruña (Northern stations). Environmental variables also appear to affect porpoise distribution: more porpoises were detected in waters where the depth of the eutrophic zone (ZEU) was higher, depth was more variable, seabed slope was greater and the continental shelf was narrower.

Finally, stranding data from 1990 to 2013 from Galicia recorded by CEMMA and from 2000 to 2013 from Portugal recorded by Sociedade Portuguesa de Vida Selvagem (SPVS) were analysed. A total of 424 strandings of harbour porpoises were recorded in the whole area. The results showed that porpoise strandings occur throughout the year, with differences between years. The highest numbers of porpoises stranded were recorded in Galicia in 1998, and in Portugal in 2011. Also differences between months were found. In Galicia porpoise strandings were more common in winter with a peak in March and in April; and in Portugal a peak in May was detected. When analysing data from both areas together, the number of strandings is higher in winter than in summer. There was an increase in the number of porpoises stranded from North to South with two regions having the most strandings: sub-areas 5 and 9. Overall, sex ratio in strandings was close to 1:1, although the number of females was slightly lower in Portugal. The total body length ranged from 81 to 202 cm with a mean length of 146.66 cm, the Portuguese porpoises being larger than Galician, and females larger than males. Overall, 33.4% of the stranded porpoises had signs of by-catch with a higher proportion in the Portuguese coast (56.0%) than in the Galician coast (26.2%), which could be due to the difference of the gears used in each area by fishermen.

Results provide evidence of an absence of genetic structure in the harbour porpoise population along the WIP and a clear isolation of this population from the populations of the North East Atlantic and Black Sea, with an important influence of the predominant oceanographic features such as currents and upwelling. These results support the recommended definition of Iberian Peninsula as a separated management unit for harbour porpoise for the MSFD and also the definition of a third subspecies, *Phocoena phocoena meridionalis*. Both sightings and strandings showed that porpoises are present in the area all year around with variations in the number of sightings between years, months and subareas, which leads us to think that they may move between areas. Thus, i) protected areas cannot be seasonal, because the species is present throughout the year, ii) Galicia is one of the key areas in the Iberian peninsula,

with four localities with particularly high occurrence of porpoises: Punta Candieira, Vilán and Touriñán Cape, Punta Remedios (Lira) and Faro de Corrubedo, iii) the main areas used by harbour porpoises and bottlenose dolphins are different. Moreover, while a part of the bottlenose dolphin population was described as a resident population, the porpoise population does not seem to behave in the same way; therefore the same SAC is not going to be useful for both species, unless it is big enough to cover those different areas.

It is well known that by-catch is one of the principal threats for small cetaceans, especially harbour porpoises, and it is of concern in an area of high fishing effort such as WIP. A higher proportion of by-caught porpoises was found on the Portuguese coast than on the Galician coasts, maybe due to the difference in the fishery arts used in each area. In any case, in both areas (Galicia and Portugal) bycatch mortality is unsustainable as the limit of mortality of 1.7 % of the best population estimate according to ASCOBANS (1997). However by-catch is not the only threat for this species, and is essential to carry out further studies to enrich the knowledge about Iberian harbour porpoises and to support its conservation.

palabras clave

Marsopa, *Phocoena phocoena,* genetica, marcadores microsatélites, ADN mitocondrial, distribución, modelización del hábitat, GAM, muestreos desde barco, muestreos desde tierra, varamientos.

resumen

El objetivo principal de esta tesis fue proporcionar información sobre la marsopa (*Phocoena phocoena*) en el noroeste de la península ibérica (NOPI), ya que está clasificadas como especie “Vulnerable” en España (Catálogo Nacional de Especies Amenazadas, Ley 4/1989, 2000; Livro vermelho dos vertebrados de Portugal) y está incluida en el Anexo-II de la Directiva Hábitats de la UE, requiriendo la designación de Areas de importancia para la Conservación (AIC) por parte de los Estados Miembros de la UE en áreas de hábitats críticos. El estudio de su población es una cuestión prioritaria y tanto la CBI (Comisión Ballenera Internacional) y el ICES (International Council for the Exploration of the Sea) recomiendan estudios que determinen la estructura poblacional y que desarrollen una gestión apropiada para reducir los impactos negativos sobre la población. Así mismo, se considera en algunos estados miembros de la EU la distribución, abundancia y dinámica poblacional de los cetáceos como indicadores de “buen estado medioambiental” de las aguas marinas de la UE bajo la Directiva Marco sobre la Estrategia Marina (DEME).

Ya que la conservación requiere un conocimiento de la distribución y estructura poblacional, aquí se examinó la estructura poblacional de las marsopas del noreste Atlántico y mar Negro usando diez marcadores ADN microsatélite y la secuenciación de la variación de la región control mitocondrial. El análisis Structure del ADN microsatélite identificó 3 grupos principales: la Península Ibérica, el resto del Atlántico noreste, y el mar Negro. El análisis de *median joining network* destacó el aislamiento de la población del mar Egeo, Mármara y Negro. Ni los DNA microsatélite ni el DNA mitocondrial detectó diferencia alguna entre Galicia y Portugal, ni tampoco patrón significativo alguno en la estructura poblacional a lo largo de la costa ibérica. En cualquier caso, hubo diferencias entre la península ibérica y el resto de las poblaciones estudiadas. Los valores de variabilidad genética en ambos marcadores fueron más bajos en la península ibérica que en el resto de las poblaciones estudiadas, excepto las del mar Egeo, Mármara y Negro. Los niveles de divergencia claramente no explican el aislamiento por distancia, pero en cambio posiblemente puede asociarse con la separación de las poblaciones por las condiciones oceanográficas presentes por la presencia de las condiciones de *upwelling* en el oeste peninsular y el noroeste de África, que proporcionan unas condiciones favorables para la marsopa. En general los datos genéticos sugieren que la península ibérica y el oeste africano deberían ser considerados como una población separada.

En segundo lugar, se usó la modelización del hábitat ya que representa una herramienta potencialmente potente para describir y predecir la distribución de los cetáceos y entender los procesos ecológicos que determinan esas

distribuciones. Se usaron dos métodos de toma de datos por la ONG CEMMA (Coordinadora para o Estudo dos Mamíferos MAriños): 1. Emarques específicos desarrollados en aguas costeras gallegas durante los años 2003 – 2010. 2. Datos del seguimiento sistemático mensual en una serie de puntos de observación distribuidos homogéneamente a lo largo de la costa gallega recogidos de 2003 a 2011. Los resultados de los embarques mostraron que: i) valores altos de estado del mar influyen negativamente en la detección de marsopas; ii) el ancho de campo de observación tiene un efecto positivo; y, iii) la mejor velocidad del barco para el muestreo de marsopas fue de 6 nudos. Hubo variabilidad interanual con un aumento significativo del número de avistamientos en 2005 y sin detecciones en 2006. Por el contrario, no hubo diferencias significativas en la presencia de marsopas entre meses o en relación a la profundidad. Se encontró que varias variables medioambientales eran significativas para explicar la presencia de marsopa: i) se vieron principalmente en aguas con temperaturas medias; ii) al aumentar la concentración de clorofila y la profundidad de la zona eutrófica, aumenta la probabilidad de presencia de marsopa; iii) finalmente, hubo una relación positiva entre el número de avistamientos y tanto la mayor pendiente de los fondos como su orientación al sur.El análisis de las observaciones costeras mostraron que cinco variables tenían alguna influencia sobre los observadores en relación a la detección de marsopas: i) la duración de la observación, y ii) el ancho de campo, tuvieron una relación positiva con los avistamietnos; iii) hubo una disminución linear en los avistamientos al aumentar los valores de Beaufort; iv) las marsopas se vieron más frecuentemente cuando los valores de Douglas estaban entre 2 y 3; y v) la presencia de delfines mulares (*Turiops truncatus*) tuvo un efecto negativo en la presencia de marsopas. Durante el periodo de estudio hubo una tendencia temporal con el aumento del número de avistamiento a lo largo de los años. Así mismo, hubo un aumento en el número de avistamientos al final del día, y el número de avistamientos aumentó hacia el norte con más detecciones en Lugo y A Coruña (estaciones más norteñas). Las variables medioambientales también parecieron afectar la distribución de las marsopas: se detectaron más marsopas en aguas con la profundidad de la zona eutrófica mayor, zonas de profundidad más variable, pendiente del fondo marino mayor y plataforma continental más estrecha.

Finalmente, se analizaron los datos de varamientos recogidos desde 1990 a 2013 por la CEMMA en Galicia y de 2000 a 2013 por la Sociedade Portuguesa de Vida Selvagem (SPVS) en Portugal. Se registraron un total de 424 varamientos de marsopa en toda la zona. Los resultados mostraron que los varamientos de marsopa ocurren a lo largo de todo el año con diferencias entre ellos. El mayor número de varamientos registrado en Galicia fue en 1998 y en Portugal en 2011. También se detectaron diferencias entre meses. En Galicia los varamientos de marsopa fueron más comunes en invierno con un pico en Marzo y Abril, y en Portugal se detectó el pico en Mayo. Al analizar conjntamente los datos de ambas zonas, el número de varamientos es mayor en invierno que en verano. Hubo un aumento de las marsopas varadas del norte al sur, teniendo dos zonas la mayoría de los varamientos: subárea 5 y 9. En general, la proporción de sexos fue cercana a 1:1, aunque el número de hembras fue ligeramente menor en Portugal. La longitud total del cuerpo varió entre 81 a 202 cm, con una longitud media de 146.66 cm, siendo las marsopas portuguesas mayores que las gallegas, y las hembras más grandes que los machos. En total, un 33.4% de las marsopas varadas tenían signos de captura accidental, con una mayor proporción en las costas portuguesas (56.0%) que en las gallegas (26.2%), lo que podría ser debido a las artes de pesca usadas en cada zona por los marineros.

Los resultados muestran evidencias de la ausencia de una estructura genética poblacional de las marsopas en la costa noroccidental peninsular y un claro aislamiento de esta población con otras del noreste atlántico y del mar Negro, con una influencia importante de las características oceánicas predominantes como las corrientes y el *upwelling*. Estos resultados apoyan la recomentación de la definición de la Península Ibérica como una unidad de gestión de marsopa

separada para el DEME y así mismo la definición de una tercera especie, *Phocoena phocoena meridionalis*. Tanto los avistamientos como los varamientos mostraron que las marsopas están presentes en el area todo el año con variaciones en el número de avistamietnos entre años, meses y subáreas, lo que nos lleva pensar que deben de moverse entre zonas. Por lo tanto, i) las zonas de protección no pueden ser estacionales, al estar la especie presente a lo largo de todo el año; ii) Galicia parece ser una de las zonas clave en la Península Ibérica, junto probablemente con el golfo de Cádiz, con cuatro localidades con una particular presencia de marsopa: Punta Candieira, Cabo Vilán y Touriñán Cape, Punta Remedios (Lira) y Faro de Corrubedo; iii) las áreas principales usadas por las marsopas y los delfines mulares son diferentes. Además, mientras que parte de la población de delín mular ha sido descrita como residente, la población de marsopa no parece comportarse del mismo modo, y por lo tanto el mismo AIC no va a ser útil para ambas especies, salvo que sea lo suficientemente grande como para cubrir ambas zonas.

La captura accidental es considerada como uno de los principales amenazas para los pequeños cetáceos, especialmente marsopas, y es preocupante en una zona de gran presión pesquera como la noroccidental peninsular. Se detectó una mayor proporción de capturas accidentales en las costas portuguesas que en las gallegas, tal vez debido al uso de distintas artes de pesca en cada zona. En cualquier caso, en ambas áreas (Galicia y Portugal) la mortalidad por captura accidental es insostenible según el límite de mortalidad del 1.7% de la mejor estima poblacional de acuerdo con ASCOBANS (1997). De todas formas, la captura accidental no es la única amenaza para esta especie, y es básico llevar a cabo más estudios para aumentar el conocimiento de las marsopas ibéricas y apoyar su conservación.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

General introduction

This thesis concerns aspects of the ecology and population structure of harbour porpoise in the Iberian Peninsula. In the present chapter the rationale for studying marine mammals is outlined and the study species and study area are described. The chapter also reviews threats to porpoises and current conservation legislation. Finally, it presents the objectives of the thesis.

The importance of studying marine mammal ecology.

There are several reasons that support the study of marine mammals beyond the increase of knowledge about the species that inhabit the marine environment. Marine mammals are apex/top predators, and have very few or no natural predators. Then, they can play an important role as *top-down regulators* of ecosystem functioning (Estes et al 1998, 2004, Williams et al 2004, Morrisette et al 2012, Santos et al 2014), and significant variation in their abundance or distribution may influence other species and ecosystem processes through a trophic cascade. The most well-known example is the one involving sea otter (*Enhydra lustris*), sea urchins and kelp forest (review in Estes 2005). Sea otters prey on sea urchins, which are the major kelp consumers. Because of the eradication of otters from vast coastal areas, sea urchins increased to a point where kelp forests were rare or had completely disappeared. This changed seascape appearance, ecosystem productivity, nutrient cycling, growth rates of mussels and barnacles and densities of several fishes. Similar effects were found in areas where killer whales (*Orcinus orca*) began to predate on sea otters, probably triggered by fisheries depletion which reduced killer whale main prey. Such change added a new top predator and trophic level to the system, leading to a decline of the sea otter population, an increase of sea urchins and, again, a depletion of kelp forests (Estes et al 1998). Some species of marine mammals are described as keystone species, due to their influence in ecosystems, i.e. a species that have an important impact on the ecosystems relative to their abundance (Paine 1980), leading some times to trophic cascade. Alteration of the marine food webs due to the decrease of a cetacean species has also been reported in the Bering Sea (Merrick et al 1997) the North Pacific Ocean (Croll et al 2006) and the Baltic Sea (Österblom et al 2007).

Also, marine mammals may be influenced by *bottom-up regulation*. Oceanic and atmospheric climate shifts affected the key species of prey consumed by Steller sea lions (*Eumetopias jubatus*) in the western Gulf of Alaska and in the Aleutian Islands (Cury and Shannon 2004), by marine birds and seals in southern Benguela (Trites et al 2007), spinner dolphins (*Stenella*

longirostris) in Hawaii (Benoit-Bird and McManus 2012) or killer whales in Northeast Pacific (Ford et al 2010) leading to a decrease in their abundance.

There are many factors that can cause changes in the abundance and/or distribution. One of the principal threats for cetaceans worldwide is interactions with fisheries, directly through bycatch (Jefferson and Curry 1994, Perrin et al 1994, Lasalle et al 2012, Read 2013), or indirectly by the overexploitation of prey, which can also have unpredictable consequences for ecosystem dynamics (Baum and Worm 2009, Navia et al 2012). Other threats include pollution, environmental changes such as climate change, ship strikes and underwater noise (e.g. Jepson and Baker, Jepson et al 1998, 2003, 2005, ACCOBAMS 2005, Cox et al 2006, Learmonth et al 2006, MacLeod et al 2009, Fernández et al 2012, IWC 2012, Lambert et al 2014).

Moreover, they are considered as sentinels because, due to their position at the top of the food chain, they are vulnerable to bioaccumulation and biomagnification, and their life history makes them vulnerable to human-induced alterations of the ecosystem. As sentinels, they may be an early warning system for contamination by chemicals (e.g. mercury, DDT (Dichlorodiphenyltrichloroethane), PCB (polychlorinated biphenyls)), climate change, changes in food webs and disease pathways (Ross 2000, Moore 2008, Burek et al 2008, Bossart 2011, ICES 2014). For example, in the North Pacific and Arctic, grey whales (*Eschrichtius robustus*) had changes in their distribution and behaviour correlated with changes in their environment (Moore 2008). Another example is the study of PCB in three species of cetaceans in the UK (Law et al 2012). Concentrations of PCBs in harbour porpoises showed a decline in the early to-mid 1990s, followed by a "steady-state" plateau (1998–present) due to regulation of use, but are still at toxicologically significant levels in many harbour porpoises and regularly occur at even higher levels in bottlenose dolphins and killer whales due to their higher trophic level in marine food chains, with the highest risk of individual and population level toxicities.

As species that usually need large areas for foraging and breeding, the area needed to protect marine mammals is expected to be also useful for species that are less demanding. Besides, marine mammals are charismatic and capture the attention and concern of the public, which can help to promote actions for their conservation and for conservation in general. They are ideal material for education and dissemination, as the general public is usually more easily captured by charismatic species than by difficult concepts. Then, they can be used as "umbrella species" or "flagship" species.

Some authors (e.g. Roberge and Angelstam 2004) suggest that the definition of an umbrella species for conservation expecting the protection of a large number of co-occurring species is not enough, as some species are limited by ecological factors that are not relevant to the umbrella species or the protection of a higher taxon may not necessarily confer protection to assemblages from other taxa. In contrast, multi-species strategies for conservation are more useful. This is the case of the "focal species" approach (Lambeck 1997), which for each landscape type, the most sensitive group of species in terms of resources, area requirements, connectivity, and natural processes should be selected. The critical habitat requirements of each focal species are used to define the amount and configuration of habitats that must be present in the landscape and are then used to help form a single management plan based around each of the causes of decline, as it assumed that because the most demanding species are selected, a landscape designed and managed to meet their needs will encompass the requirements of all other species similarly threatened. This multi-species approach is not usually used in marine environments and shows several limitations (Zacharias and Roff 2001): the spatial and temporal variation in many marine communities and most species are generalist (while exhibiting prey preference), the requirement that an umbrella species be non-migratory and the assumption that protecting generalist feeders will protect other species associated with the generalists may be an unwise management approach.

In any case, marine mammals are an excellent candidates to be indicators of the condition of the marine environment, fulfilling many of the criteria defined by International Council for the Exploration of the Sea (ICES 2001), Marine Strategy Framework Directive (MSFD) (Directive 2008/56/EC) and OSPAR (2012) to be good bioindicators of Good Envrionmental State (GES).

The harbour porpoise (*Phocoena phocoena*).

Phylogeny and distribution.

There are six species of porpoises (Family Phocoenidae), and the harbour porpoise, *Phocoena phocoena* (Linnaeus 1758), is one of the three recognized species of the genus *Phocoena* (Read 1999): *Phocoena phocoena phocoena, P. p. relicta* and *P. p. vomerina*. It is one of the smallest cetaceans and has a wide distribution in coastal and continental shelf temperate and subarctic waters of the Northern Hemisphere (Gaskin 1984, Read 1999); it has also been reported in deep oceanic waters between major land masses (Donovan and Bjørge 1995, NAMMCO 1998, 2013, Teilmann and Dietz 1998, Skov et al 2003, Read and Westgate 1997).

Figure 1. Harbour porpoise (*Phocoena phocoena*) adult and calve (drawing by Tokio).

Three subspecies have been differentiated based on their isolated distributions: *P. p. phocoena* in the North Atlantic, *P. p. relicta* in the Black Sea, and *P. p. vomerina* in the Pacific (Fig. 2). Variations were also found in morphometric data (Kinzie 1985, Miyazaki et al 1987, Yurick and Gaskin 1987, Amano and Miyaza 1992, Gol'din 2004, Viaud-Martinez et al 2007, De Luna et al 2012) and genetics (Rosel et al 1995, Viaud-Martinez et al 2007, Fontaine et al 2010, 2012).

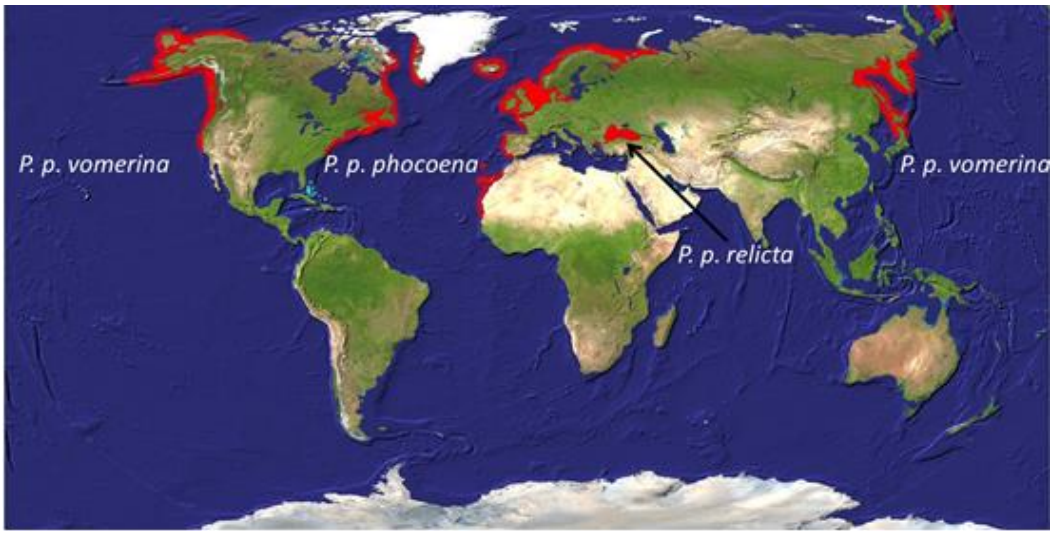


Figure 2. Distribution of the three subspecies of harbour porpoise (created from: http://www.vertebradosibericos.org/mamiferos/distribucion/phophodi.html, http://www.nmfs.noaa.gov/pr/pdfs/rangemaps/harborporpoise.pdf, http://maps.iucnredlist.org/map.html?id=17027).

In the Eastern North Atlantic, harbour porpoise is found from Spitsbergen, North Norway (77° N; Bjørge and Øien 1995) to Senegal coast at West Africa (20° N; Boisseau et al 2007). Along the Atlantic coast from France in 1990s it was considered "rare" but a recovery was detected since 1999 (Jauniaux et al 2002, Jung et al 2009, Alfonsi et al 2012). There is also an apparent distribution gap from the Strait of Gibraltar to Agadir, central coast of Morocco (Van Waerebeek 2007, Boisseau et al 2007). In the Macaronesia region, Barreiros et al (2006) reported a stranding at Terceira Island that led the authors assume the existence of a local population in Azorean waters but, despite coastal and offshore monitoring and the existence of a regular whale-watching industry on several islands, there have been no other records (Silva et al 2014). Harbour porpoises were also recorded around the Canary Islands as vagrants (Martin et al 1992, Carrillo 2007), but there are no records from Madeira.

It is considered extinct in the Mediterranean Sea (Gaskin 1984, Blanco and Gonzalez 1992, Frantzis et al 2001), although it is present in the Aegean Sea (Güçlüsoy 2009, Frantzis et al 2001, Tonay and Dede 2013), and Marmara Sea (Dede et al 2008, Ozturk et al 2009, Tonay et al 2009, Güçlüsoy 2009). The presence of porpoises in the Aegean Sea could be explained by the dispersion of the species from the Black and Marmara Seas, which is the most likely explanation, or it could be a remnant of the population that was formerly dispersed more widely through the Mediterranean Sea (Frantzis et al 2001).

Abundance.

Together with the distribution, the estimation of the abundance of the population is important as a measure of population status, for the determination of the effect of stressors, the establishment of Protected Areas, development of management plans and evaluation of whether conservation measures are effective.

There are different methods to obtain data on cetaceans for the study of abundance. Most of these methods are based on visual observation. Observations can be made from boat, land and plane (e.g. Evans and Hammond 2004). There are however several problems with visual observation, for example observers can see cetaceans only during the very short period when they are at the surface, and it is dependent on daylight hours and good weather conditions. These limitations are not present in acoustic monitoring that allows data collection at night and under bad weather conditions, but the calculation of abundance from acoustic data is controversial as animals can be "quiet" and thus not recorded, it is difficult to determine the number of individuals acoustically, and the incorrect identification of the species can be problematic (Oswald et al 2007, Mellinger et al 2007, Marques et al 2009, 2011, Caillat et al 2013).

The estimation of the abundance of a highly mobile species such as harbour porpoise (Read and Gaskin 1985, Westgate et al 1995), a species that also shows seasonal movements (Keiper et al 2005, Siebert et al 2006, Verfuß et al 2007, Scheidat et al 2008, 2011, 2012, Gilles et al 2009, Camphuysen 2011, Haelters et al 2011, Heide-Jørgensen et la 2011, Sveegaard et al 2011, Geelhoed et al 2013, Benke et al 2014), must be carefully calculated to account for its movements between different areas.

Various studies have been carried out to estimate the abundance of porpoises in areas of the North East Atlantic (Gillespie et al 2005, Berrow et la 2007, Shucksmith et al 2008, Healters and Camphuysen 2009, Gilles et al 2011, Haelters et al 2011, Leeney et al 2011, Scheidat et al 2012, Geelhoed et al 2013, Benke et a 2014). Two large-scale surveys (SCANS and SCANS II) were carried out during summer months, mainly in July, of 1994 and 2005 (Hammond et al 2002, 2013). In the first survey, the porpoise population was estimated to be 341000 individuals (Hammond et al 2002) in the North Sea and adjacent waters and in a comparable area in 2005, the estimate was 324000 (Hammond et al 2013). Whereas there was no significant difference in abundance estimations, there was a marked difference in porpoise distribution with a shift from northwest to the southwest in the North Sea. This movement was also detected in other

more localised studies (Jauniaux et al 2002, Camphuysen 2004, Gilles et al 2009, 2011, Healters et al 2011, Scheidat et al 2012, see Fig. 3 from Hammond et al 2013).

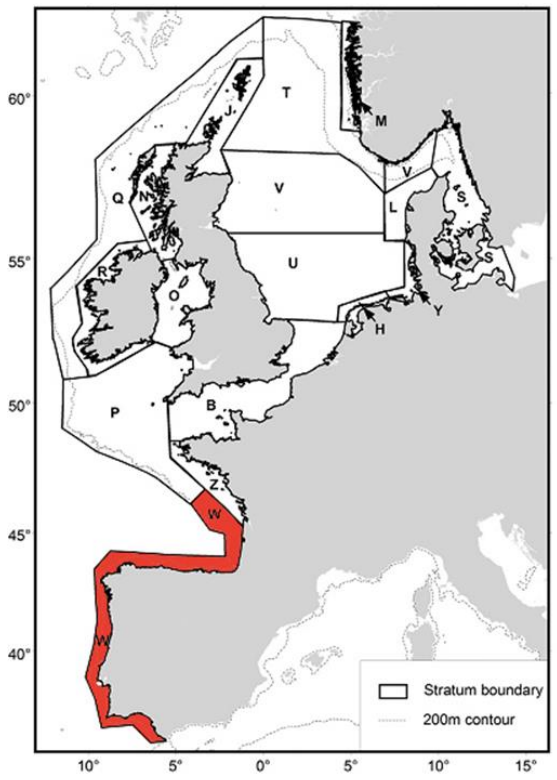


Figure 3. Survey blocks defined for the SCANS-II surveys modified from Hammond et al (2013). Block W, which comprises Southwest France, Spain and Portugal, is highlighted in red.

Diet.

Harbour porpoise is a fish feeder that tends to feed primarily on two to four main species in any one area (Santos and Pierce 2003). The most important prey types in Scottish waters were whiting (*Merlangius merlangus*) and sandeels (Ammodytidae) (Santos et al 2004). In Denmark the main prey were cod (*Gadus morhua*), viviparous blenny (Zoarcidae) and whiting. In the Netherlands more than 75% of the total estimated prey weight corresponded to whiting although gobies dominated the diet in terms of numbers eaten (88% of the total) (Santos et al 2005). In Normandy, Gobiidae made up more than 95% of prey collected in the stomachs (De Pierrepont et al 2005) whereas scads (*Trachurus trachurus* or/and *T. mediterraneus*), sardine (*Sardina pilchardus*), blue whiting and whiting were found to be the main prey along the Northeast Atlantic French coast (Spitz et al 2006). In Iceland (Víkingsson et al 2003), the predominant prey was capelin (*Mallotus villosus*). In Galicia studies of the stomach contents of stranded and by-catch porpoises identified 18 fish taxa and four cephalopod taxa. *Trisopterus*

spp were the main prey, followed by blue whiting (*Micromesistius poutassou*) and *Trachurus* spp (Read et al 2012, Pierce et al 2010). In Portugal the principal prey was the common dragonet (*Callionymus lyra*), followed of *Trisopterus* sp. and *Liza* sp. (Aguiar 2013). Variation in diet depending on the region, season and year of study, and body size, were found at Scotland and Portugal (Santos et al 2004, Aguiar 2013).

Harbour porpoises are one of the smallest cetacean species and their small body size means that they cannot store much energy and they can only survive very short periods without feeding (as little as 3 days) (Kastelein et al 1997). Although the reproductive interval is estimated to vary from 1 to 2 years in eastern Atlantic (Lockyer 2003, Lockyer and Kinze 2003, Ólafsdóttir et al 2002, Read et al 2012), in the western Atlantic, mature females often are pregnant and lactating at the same time (Read et al 1997). Those factors together suggest that they are more dependent on a year-round proximity to food sources than other cetacean species (Brodie 1995).

Lockyer et al (2003) found a marked variation in food intake throughout the year. Yasui and Gaskin (1986) estimated a food daily consumption of 3.5% of total body weight, Kastelein et al (1997) of 4 – 9.5%, and Santos et al (2014) based on the information of Yasui and Gaskin (1986) and Kastelein et al (1997), of 4.44%. In the same study, the consumption of sardine by common, striped and bottlenose dolphin and harbour porpoise in Iberian Atlantic waters was estimated to represent between 3% and 6% of the current estimate of natural mortality of sardine, the predation by bottlenose dolphin and porpoises being less than 1% of the total removal of sardine by these four species. For hake, harbour porpoise predation only represents around 1% of total amount of hake consumption by cetaceans.

New techniques have been developed to study the diet and foraging habits. These techniques include the study of stable isotopes (such as nitrogen $\delta^{15}N$ and $\delta^{13}C$ carbon) and Cd. Mean values of $\delta^{13}C$ in Black sea porpoises were found to be different between males and females, suggesting a trophic segregation between sexes, with females having a more coastal distribution, and hepatic Hg was found to be correlated with $\delta^{13}C$ reflecting the difference between coastal and offshore feeding habitats (Das et al 2004 a). Sexual segregation in diet was also found for Dutch (Das et al 2003, Jansen et al 2012, Christensen and Richardson 2008) and French and Belgian porpoises (Das et al 2003). In Scandinavian waters, only Cd, among the trace elements analysed, was found to be useful as ecological tracer for food origin (Fontaine et al 2007 b). Measures of this trace element suggest that porpoises in northern waters include

more oceanic cephalopods in their diet, and together with $\delta^{13}C$ and $\delta^{15}N$ show a shift in harbour porpoise feeding habits from pelagic prey species in deep northern waters to more coastal and/or demersal prey in the relatively shallow North Sea and Skagerrak waters. Studies focusing on harbour porpoises and bottlenose dolphins (*Tursiops truncatus*) found a partial dietary overlap of their foraging niche in the Bay of Biscay (Spitz et al 2006), suggesting a potential competition for limited resources. Méndez-Fernandez et al (2013) analysed stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) and Cd as ecological tracers to study the niche segregation of the 5 main species at the Iberian Peninsula (common dolphin (*Delphinus delphis*), bottlenose dolphin, harbour porpoise, striped dolphin (*Stenella coeruleoalba*) and long-finned pilot whale (*Globicephala melas*)) and found that porpoises have a coastal foraging niche with the highest trophic position among the studied species. Bottlenose dolphins have a similar foraging niche to porpoises, but with a lower trophic position, which suggest that they have different prey and/or the use of offshore areas.

Life history.

Longevity in harbour porpoises is up to 23 years in both sexes, but less than 5% of the individuals live more than 12 years (Lockyer 1995, 2003, Lockyer and Kinze 2003, Learmonth et al 2014).

For harbour porpoises the sex ratio does not change significantly between age classes, with a slightly larger proportion of males seen than females (Lockyer 2003, Lockyer and Kinze 2003, López 2003, Ólafsdóttir et al 2002, Read et al 2012). Harbour porpoise females show larger sizes than males (Gaskin 1984, Read 1999). In the North Atlantic, lengths in females vary between 153.4 and 163 cm, and males between 141.1 and 148.8 cm, although their body size varies with geographic location, the West Greenland porpoises being the smallest and the Iberian porpoises the largest (Table 1; Sequeira 1996, Lens 1997, López 2003, Lockyer et al 2003, Read et al 2012, Learmonth et al 2014). Mean body weight for females is between 34 - 47 kg, and 27 - 35 kg for males, with females being heavier than males, with some females attain weights of up to 89 kg (Lockyer and Kinze 2003) and 79.5 kg for males (Lockyer 1995, Lockyer and Kinze 2003).

Its sexual maturity is estimated to occur at between 3 and 4 years old in both sexes, and at about 135 cm length in males, and at 140 cm in females, although there is some regional variation (Sorensen and Kinze 1994, Lockyer 2003, Lockyer and Kinze 2003, López 2003, Ólafsdóttir et al 2003, Read et al 2012, Learmonth et al 2014).

The reproductive interval is estimated to vary from 1 to 2 years (Lockyer 2003, Lockyer and Kinze 2003, Ólafsdóttir et al 2002, Read et al 2012). In Scotland, there were lower estimates of reproductive rate in porpoises and mature females may become pregnant only once every 2.5 – 3 years, although this result could be underestimated because the study was based on stranded animals, among which there were relatively few mature females and of the mature females most of them were with poor health (Learmonth et al 2014). The gestation period is estimated to be of around 10 – 11 months (Sorensen and Kinze 1994, Learmonth et al 2014). Reproduction is very seasonal in all populations of harbour porpoises, with parturition occurring in North Atlantic mainly between June and July, although in Scottish waters it is estimated to be between April and July, and in Iberian Atlantic waters it seems that this period is not so defined with a first peak in spring and a second one in summer (Barreiro et al 1994, Sorensen and Kinze 1994, Lockyer 1995, 2003, Sequeira 1996, Read 1999, López 2003, López et al 2012, Silva et al 1999, Learmonth et al 2014). At birth they are between 60 and 75 cm of length and 3.4 – 6.7 kg of weight (Lockyer and Kinze 2003) and lactation is probably at least 8 months (Lockyer 2003).

Population structure.

In the Northeast Atlantic and adjacent seas, genetic studies using several markers (e.g. allozymes, RFLP of mitochondrial DNA, mitochondrial DNA sequencing, microsatellites or a combination of markers), distinguish three different populations: 1) Northeast Atlantic from France to Norway (including the Baltic porpoises) as a “continuous” population with significant isolation by distance (Fontaine et al 2007) without a clear population structure, 2) Iberian Peninsula and West Africa, 3) Black Sea (e.g. Andersen et al 2001, Tolley and Rosel 2006, Fontaine et al 2007 a, Wiemann et al 2010, Alfonsi et al 2012). In relation to conservation efforts under the MSFD, these areas were divided in five management units: Celtic and Irish Seas, Iberian Peninsula, West Scotland and Northern Ireland, North Sea and Kattegat and Belt Seas (ICES 2013, Fig. 4). Strong barriers to gene flow split this population from the Iberian and West Africa population, with a restricted admixture zone in the Bay of Biscay (Fontaine et al 2007 a, 2014, Alfonsi et al 2012).

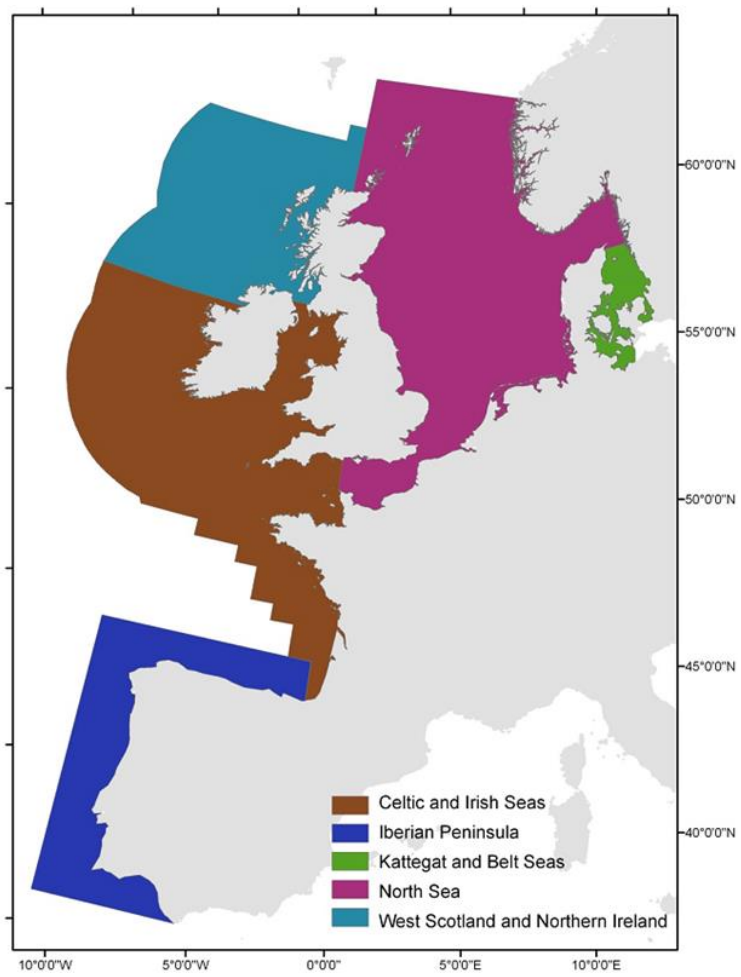


Figure 4. Map showing recommended management units for harbour porpoise proposed for MSFD (WGMME 2013).

The animals from Spain and Portugal are a genetically homogeneous group with a gene flow from Iberia to West Africa (Tolley and Rosel 2006, Viaud-Martinez et al 2007, Fontaine et al 2012).

Finally, porpoises from the Black Sea underwent historical isolation because of environmental changes in the Mediterranean Sea (Tolley and Rosel 2006, Fontaine et al 2010), where nowadays the species seems to be absent (Frantzis et al 2001), leading to a genetic isolation confirmed by several studies (e.g. Rosel et al 1995, 2003, Andersen et al 2001, Tolley and Rosel 2006, Fontaine et al 2007 a, 2010, Wiemann et al 2010). Within this area, no significant differences were detected between porpoises from the Aegean and Black Sea (Fontaine et al 2012), which suggests that Aegean porpoises come from Black Sea rather than from the Atlantic population (Rosel et al 2003, Tonay et al 2012).

Together with morphological data (Sequeira 1996, López et al 2003, Rosel et al 2003, Gol'din 2004, Viaud-Martinez et al 2007, Galatius and Gol'din 2011, Read et al 2012), genetic data contribute to the description of three subspecies: *P.p. phocoena* in the North Atlantic, *P.p. meridionalis* in Iberia and West Africa and *P.p. relicta* in the Black Sea (Gaskin 1984, Rosel et al 1995, Fontaine et al 2014) and the definition of 5 management units in European Northeast Atlantic (ICES 2014).

Threats.

The Marine Strategy Framework Directive (Directive 2008/56/EC) mentioned five different reasons why European Seas were not considered to be at "good environmental status":

1. Marine ecosystems face increasing pressure from human activities both on land and at sea, as 41% of the European population live in coastal regions and economic activities depending on the marine environment are growing.
2. 39% of (fish) stocks in the Northeast Atlantic and 88% in the Mediterranean and Black Seas are still overfished and the situation is improving only slowly.
3. Pollution in the marine environment has decreased in some places but levels of nutrients and certain hazardous substances are overall still above acceptable limits. Oxygen depletion, as a result of nutrient pollution, is particularly serious in the Baltic and Black Seas.
4. Marine litter, mostly plastic, is a growing issue globally and in the EU. In the North Sea, over 90% of fulmars have plastic in their stomach and on average 712 items of litter are found per 100 m stretch of beach on the Atlantic Coast. The impacts of this increasing problem are manifold and their magnitude not yet fully known.
5. Climate change, though not directly assessed under the MSFD, also contributes to the further degradation of marine ecosystems.

All these issues are relevant to cetaceans such as porpoises but the second one (fishing pressure) probably represents the most serious threat to porpoises, due to high levels of fishery bycatch mortality of porpoises in certain fisheries.

<u>By-catch.</u>

By-catch is one of the principal threats for small cetaceans, especially harbour porpoises (IWC 1994), being the most frequent known causes of death of North Sea porpoises together with

acute bronchopneumonia (Baker and Martin 1992, Kuiken et al 1994, Kirkwood et al 1997). In the UK, by-catch was the cause of death 34% of the stranded porpoises that were examined (Jepson et al 2000), in Germany 46% (Siebert et al 2001), in North West Spain 49.4% (López et al 2012) and in Portugal around 58% of the porpoises (Ferreira 2007). The precise nature of the interaction varies between areas, fishing gear type, cetacean species, cultures, and any combination of these (IWC 1994). ASCOBANS has advised that bycatches should not exceed 1.7% of the best population estimate. By-catch can be estimated from: i) the number of by-caught animals recorded by observers on board in a representative sub-sample of a fishery, ii) stranding, iii) interviews with fishermen, and, iv) animals landed by fishermen. In strandings, bycatch can be diagnosed using signs such as net marks, which are normally confined to the front of the pectoral flipper, dorsal fin and fluke, or the head region, mutilations, and/or cuts on the ventral side (Kuiken et al 1994, Siebert et al 1999, 2006, Ferreira 2007). Porpoises are taken incidentally in several different gear types (driftnets, trammel, trawl nets, etc), but mostly in bottom-set gillnets (Read 1999).

There are several methods to mitigate marine mammal bycatches (Bjørge et al 2012, Ophranides and Palka 2013, Read 2013) including:

i) acoustic alarm devices (pingers). Eleven EU Member Countries are affected by the monitoring and mitigation requirements of Council Regulation (EC) No.812/2004, although not all are carrying out any action. For example, “Pingers” were used in Sweden, Denmark, Germany, Ireland, Latvia, Poland, and the United Kingdom but overall effectiveness of the mitigation could not be evaluated because of the lack of data (and because the EU does not require monitoring of the effectiveness of those measures) (ICES 2014). Pingers have proven efficient in several experiments (e.g. Palka et al 2008, Gazo et al 2008, Carlström et al 2009, Gönener and Bilgin 2009, Northridge et al 2011, Ophranides and Palka 2013, Dawson et al 2013). However, there are still concerns about their practicality and effectiveness over the long term, and their negative impacts from the noise they emit (Cox et al 2001, Claström et al 2002, 2009, Cox and Read 2004, Gazo et al 2008, Kyhn et al 2015).
ii) time/area fishery closures or avoidance of fishing areas where cetaceans are present (e.g. Murray et al 2000). This has its limitations as there will almost certainly be an overlap between cetacean feeding areas and preferred fishing grounds (Goetz et al 2014).

iii) technological modifications to the fishing gear such as barium sulphate-enhanced or gillnets, iron-oxide gillnets (e.g. Mooney et al 2007, Trippel et al 2003, 2008, Larsen et al 2007). This method could be less efficient than acoustic alarms in controlled tests, but they are silent, do not require an external power source and are otherwise operationally identical to standard nylon gillnets (Trippel et al 2008).

Despite some progress in reducing bycatch mortality due to use of pingers on gill nets, bycatch is still considered a major threat to porpoises in European seas (ICES 2015).

Contaminants.

The OSPAR list of Chemicals for Priority Action (OSPAR 2010) cited the persistent organic pollutants (POPs) as one of the primary pollutants of concern in marine ecosystems, including (PCBs) and pesticides (e.g. DDT). Although their production has been banned since the end of the 1970s, high PCB concentrations are still found in wildlife and other environmental components (OSPAR 2010), such as porpoises in UK waters (Law et al 2012). Other classes of organic chemicals are also of concern nowadays, notably the brominated diphenyl ether formulations (PBDEs) (de Boer et al 1998) and the hexabromocyclododecanes (HBCDs) another brominated flame retardant (e.g. Zegers et al 2005, Law et al 2012). While PBDE concentrations are declining in the UK (Law et al 2010, 2012), and for both PCB and PBDEs in the North Sea, except for calves, (Weijs et al 2010), in UK HBCD levels experienced an increase between 2000 and 2001, but then showed a significant fall in concentrations after 2003 (Law et al 2012), and a decreasing trend in the North Sea from 1990 until 2008 (Weijs et al 2010).

The threshold level above which there are health effects in mammals (Kannan et al 2000) for PCBs was found to be frequently exceeded in porpoises from North Sea (74% of individuals), Ireland (25%) (Pierce et al 2008) and Iberia (75%) (Méndez-Fernandez et al 2014 a). In the UK porpoises which died due to infectious disease were found to have concentrations of PCBs higher than the porpoises that died of physical trauma (Jepson et al 2005, Law et al 2012), often also exceeding that threshold. Murphy et al (2010) also found that high PCB burdens tended to be associated with the reduction of reproductive success in females and lower survival of their first offspring during early lactation (see also Murphy et al 2015).

Many trace elements occurring in the marine environment are potentially toxic, even at low concentrations (Chappuis 1991). These elements are derived from both natural and anthropogenic (e.g. mining and industrial discharges) sources and can be divided into non-

essential elements (Cd, Pb, Hg and Ag) that are toxic elements for which no biological function has been demonstrated so far, and essential elements (Fe, Cu, Co, Zn, Se and Cr) with a biological function and whose deficiency induces pathology in humans and more generally in mammals (Chappuis 1991, Underwood 1977). Marine mammals, as long-lived apex predators, are potentially threatened by non-essential trace elements, since most are bioaccumulated and biomagnified through food webs (Law 1996, Das et al 2003), although Caurant et al (2006) did not find an apparent influence of habitat on bioaccumulation for Pb in harbour porpoises from Bay of Biscay. Heavy metal concentrations in marine mammals depend not only on environmental contamination, but also on several biological and ecological factors such as age, body condition, diet and the capacity to excrete these elements (Caurant et al 1994, Law 1996, Aguilar et al 1999, Bennett et al 2001, Das et al 2003, 2004 b, Pierce et al 2008, Méndez-Fernández et al 2014 a, b).

The toxic effects of many trace elements remain unclear (Law 1996), but comparing porpoises that died as a consequence of physical trauma (most frequently entrapment in fishing gear), and porpoises died due to infectious diseases caused by parasitic, bacterial, fungal and viral pathogens, mean liver concentrations of Hg, selenium (Se), the Hg:Se molar ratio, and zinc (Zn) were significantly higher in the porpoises of the second group than of the first one (Bennett et al 2001). A similar finding was reported by Siebert et al (1999) who report an association between both liver Hg and MeHg (monomethylmercury) concentrations with the severity of disease in harbour porpoises found in the German waters of the North and Baltic Seas. Das et al (2004 b) explains that although facing limited toxicological risk when in normal healthy condition, with deteriorating body condition, the porpoises could well be adversely affected by Zn and Hg.

Climate change.

Climate change is another threat that must be kept in mind as it seems to affect the composition and structure of ecological communities: if local conditions change, new species may join communities while others may disappear from them or change in their relative and absolute abundances (Genner et al 2004, Learmonth et al 2006, MacLeod et al 2005, 2009, Lambert et al 2014). Water temperatures have already increased due to the effects of global climate change and are predicted to continue increasing throughout much of the world's oceans (Levitus et al 2000, Barnett et al 2001, Learmonth et al 2006, Cubasch et al 2013).

For cetaceans ecological niches seem to be primarily defined by water temperature, water depth, factors that affect the distribution and abundance of their prey, so that increased temperatures are expected to have negative consequences for the conservation status of individual species (Learmonth et al 2006, MacLeod et al 2009, Lambert et al 2011, 2014). While warmer water species may benefit through an expanded range as temperatures increase, the opposite will happen for colder water species resulting in a reduction in the total area where they occur; and finally, any changes that occur in community structure may affect the ability of a conservation strategy based on the previous population structure (MacLeod et al 2005, Robinson et al 2009, Lambert et al 2011). Indeed, some populations may become locally extinct in those areas of conservation.

The distribution of several cetacean species has already changed possibly due to climate change, among other causes (e.g. MacLeod et al 2005, 2009, Heide-Jørgensen et al 2002, 2011, Newson et al 2009, Laidre et al 2008, Schumann et al 2013, Lambert et al 2011, 2014, Víkingsson et al 2014). In the harbour porpoise climate change may result in potentially harmful changes in distribution, abundance and migration, diet, body condition, increases in the susceptibility to disease and contaminants, and reductions of the reproductive success (Learmonth et al 2006, MacLeod et al 2009, Heide-Jørgensen et al 2011, Schumann et al 2013).

Noise pollution.

Noise levels in the oceans have increased considerably since engine-powered shipping was introduced in the late 18th century. Also the use of military sonar in naval exercises apparently caused mass strandings of beaked whales (Simmonds and Lopez-Jurado 1991, Frantzis 1998, Balcomb and Claridge 2001, Jepson et al 2003, 2005, Fernández et al 2005, 2012, Cox et al 2006). Evidence of acute and chronic tissue damage in stranded cetaceans that results from the formation *in vivo* of gas bubbles were found in the whales stranded in Canary Islands in 2002 (Jepson et al 2003, Fernández et al 2005), it has been detected also in other species such as Risso's dolphins (*Grampus griseus*), common dolphins (*Delphinus delphis*) and also harbour porpoises (*Phocoena phocoena*). Therefore, the use of active sonar may affect harbour porpoise adversely as well (Jepson et al 2005)

Recently other sources of anthropogenic noise have been added in the ocean, such as offshore wind farms (Tougaard et al 2009), and seismic surveys.

The growth of offshore wind farms has raised concerns about their impact on the marine

environment. Marine mammals use sound for foraging, orientation and communication and are therefore possibly susceptible to negative effects of man-made noise generated from constructing and operating large offshore wind turbines (Madsen et al 2006). If something is keeping a porpoise away from a particular area it may cause a decrease in the amount of food that is accessible to the porpoise, or alternatively it may result in the creation of a barrier between different areas that are essential to the animal at different times (Nabe-Nielsen et al 2011).

It has been shown that the harbour porpoise may react to the construction and operation of offshore wind farms in three ways:

i) positively: although the reasons are not clear, it could be an increased food availability inside the wind farm (reef effect), the absence of vessels in an otherwise heavily used part of the sea (sheltering effect), and/or a possible reduction in the fishing intensity in wind farm areas (Nabe-Nielsen et al 2011, Scheidat et al 2011);
ii) negatively: avoiding the area, changing movements, population dynamics or behaviour (Carstensen et al 2006, Gilles et al 2009, Thompson et al. 2010, Teilmann and Carstensen 2012, Dähne et al 2013, Nabe-Nielsen et al 2014);
iii) absence of an obvious behavioural reaction (Tougaard et al 2009, Nabe-Nielsen et al 2011).

If a development of a marine renewable energy is placed in, or adjacent to, sensitive areas for cetaceans, such as those used for breeding, nursing, feeding or migration, the impacts are likely to be greater than other impacts located away from these critical areas (James 2013). Brandt et al (2011) recommend the need for mitigation measures such as the use of bubble curtains and scaring devices to prevent individuals from the risk of injury from pile driving operations. However, they may reduce the risk of exposing nearby animals to damaging sound pressure levels, but will not change the fact that animals in a large area are likely to be affected behaviourally (Madsen et al 2006).

Noise can cause hearing loss which can either be temporary (TTS or temporary threshold shift) or permanent (PTS or permanent threshold shift). Also, animals can suffer masking effects (interfering or obscuring effects of noise, which limits animals from hearing signals important to them and is especially important in mysticetes that are thought to communicate over large distances of ocean or in odontodetes interfering with short-range communication and prey

finding), or fatal effects (strandings and finally, death) (e.g. Nowacek et al 2007, Weilgart 2007).

High intensity military sonar was demonstrated to have a direct relationship with atypical mass strandings of beaked whales (Frantzis 1998, Jepson et al 2003, Fernández et al 2005, 2012, Arbelo et al 2013). Those animals had chronic and acute damage in their tissues due to the formation of air bubbles such as those caused in decompression sickness (Jepson et al 2003, Fernandez et al 2005, 2012). However, other cetacean species may also be involved. Also seismic surveying activities may impact on different marine mammal species (Engel et al 2004, Gordon et al 2004).

ASCOBANS (Agreement on the Conservation of Small Cetaceans in the Baltic, North East Atlantic, Irish and North Seas) suggest that a reduction of disturbance might be achieved by continuing to collect information on seismic surveys, and continuing the dialogue with the seismic industry and military authorities on preventing/mitigating the impact of seismic activities and other noise-producing tests (ASCOBANS 2000).

Conservation measures and conservation status.

Spain.

The Ministerio de Medio Ambiente (Environmental Ministry of Spanish Government) Order of May 10th 2000 includes the harbour porpoise in the Catálogo Nacional de Especies Amenazadas (National List of Threatened Species), Ley 4/1989, as "vulnerable", what requires the elaboration of Special Management Plans for Conservation (last revision R.D. 139/2011, February 4th 2011).

In the Decreto 88/2007, Arpil 19th, that regulates the Catálogo Gallego de Especies Amenazadas (Galician List of Threatened Species), DOG Nº 89, May 9th 2007., Annex II, the harbour porpoise is listed as "vulnerable". The Decree establishes the actions needed to begin the Management Plans: the general objectives, purpose of the plan, definition of areas of interest, especially those principals for the conservation of the species due to their significance for the species to conserve, conservation measures for the species and its habitat, investigation, information, environmental education and social participation, validity and revision of the plan and additional information.

The Real decreto 1997/1995, December 7th, is the transposition to the Spanish legislation, of the Habitat Directive, which establishes the actions to guarantee the biodiversity through the conservation of the natural habitats and the wild fauna and flora.

Portugal.

The catch, transport or deliberate killing of marine mammals is forbidden by the Decreto Lei n.º 263/81, September 3rd. Also, marine mammals commercialization at any market, of animals that are either found dead in fishing gears or found stranded at the coast, is forbidden.

In Portuguese legislation, the Habitat Directive transposition is the Decreto Lei 140/99, April 24th, and the Decreto Lei 49/2005, February 24th.

International.

INTERNATIONAL UNION FOR CONSERVATION OF NATURE (IUCN)

The European Red List is a review of the conservation status of c. 6.000 European species. The European Red Lists identify those species that are threatened with extinction at the European level, and so appropriate conservation action can be taken to improve their status. 21.7% of cetaceans of the EU are considered threatened and none is classified as extinct, although 44% of the species are not well known. Harbour porpoise is classified as “Vulnerable”.

HABITATS DIRECTIVE (92/43/EEC)

The Habitats Directive (together with the Birds Directive) forms the cornerstone of Europe's nature conservation policy. It is built around two pillars: the Natura 2000 network of protected sites and the strict system of species protection. The main aim of this Directive is to promote the maintenance of biodiversity, taking account of economic, social, cultural and regional requirements. It aims to ensure the conservation of a wide range of rare, threatened or endemic species. Some 200 rare and characteristic habitat types are also targeted for conservation in their own right. In this Directive, the harbour porpoise is included in Annex II, which requires the designation of Special Areas of Conservation, and in Annex IV, in which species of Community interest in need of strict protection are listed.

MARINE STRATEGY FRAMEWORK DIRECTIVE

The MSFD aims to achieve Good Environmental Status (GES) of the EU's marine waters by 2020 and to protect the resource base upon which marine-related economic and social activities depend. The Directive enshrines in a legislative framework the ecosystem approach to the management of human activities having an impact on the marine environment, integrating the concepts of environmental protection and sustainable use. In order to achieve GES, each Member State is required to develop a strategy for its marine waters (or Marine Strategy). By 2013 Member States had reported under the Marine Strategy Framework Directive on the state of the environment in their marine waters, on what they consider as being a GES and on the objectives and targets they have set themselves to reach it by 2020 (articles 8, 9 and 10 of the MSFD).

Although Portugal has reported on GES for all descriptors (eleven qualitative descriptors which describe what the environment will look like when GES has been achieved), its report is unclear with regard to the definition of GES and there are insufficient details provided so as to evaluate if and when GES is achieved. Marine mammals were excluded due to the "lack of sufficient information", although in reality the state of knowledge of cetaceans in Portuguese waters is similar to that in Spain. Spain developed marine strategies for each of the 5 sub-divisions (North Atlantic division, South Atlantic division, Estrecho and Alborán division, Levantino-Balear division, Macaronesia (Canary) division) and there are three framework documents applicable to all sub-divisions: one general, one on marine mammals and one on birds.

The knowledge about distribution, abundance and population dynamics on cetaceans is generally considered as one of the indicators of a GES by the MSFD. Due to the growing anthropogenic impact on the health of marine environment and its natural resources (European Commission 2014), the MSFD required achieving a GES of EU's marine waters by 2020.

REGULATION 812/2004.

This regulation, which concerns the incidental catches of cetaceans in fisheries, came into force on 26th April 2004. This Regulation pursues a double objective. Firstly, it introduces technical measures concerning gill nets and trawls in specified areas. Secondly, it creates a monitoring system on board fishing vessels to obtain information on by-catches of cetaceans

in certain “at risk” fisheries. This Regulation makes the use of acoustic deterrent devices obligatory for all vessels of 12 metres or longer fishing in the zones, during the periods and using the gear listed in Annex I. However, its provisions generally exclude all small vessels, many fleets have no monitoring at all, and the monitoring of the efficacy of mitigation measures is non-existent. Added to this, several EU nations, including Spain, do not fulfil their obligations under this regulation.

IINTERNATIONAL WHALING COMMISSION (IWC)

The International Whaling Commission (IWC) is the global intergovernmental body charged with the conservation of whales and the management of whaling. It is set up under the International Convention for the Regulation of Whaling signed in 1946. In 1986 the Commission introduced zero catch limits for commercial whaling. This provision is still in place today, although the Commission continues to set catch limits for aboriginal subsistence whaling and for “research”. As well as keeping whale catch limits under review, the Commission works to promote the recovery of depleted whale populations by addressing a range of specific issues. These include ship strikes, entanglement events, environmental concerns and establishing protocols for whale watching. The Commission has agreed that the Scientific Committee can study and provide advice on small cetaceans and the Committee has established a sub-committee on small cetaceans which has operated since 1979. Each year the Scientific Committee, through its sub-committee on small cetaceans, identifies priority species/regions for review. Topics considered under such reviews include distribution, stock structure, abundance, seasonal movements, life history, ecology, status, potential threats and directed and incidental takes.

INTERNATIONAL COUNCIL FOR THE EXPLORATION OF THE SEA (ICES)

ICES is an intergovernmental organization whose main objective is to increase the scientific knowledge of the marine environment and its living resources and to use this knowledge to provide advice to competent authorities. ICES Science and Advice considers both how human activities affect marine ecosystems and how ecosystems affect human activities. It has two Working Groups directly concerned with marine mammal conservation, the Bycatch Working Group (WGBYC) and the Marine Mammal Ecology Working Group (WGMME) and is currently working to develop a mechanism to include bycatch of protected species into its fishery advice.

CONVENTION ON MIGRATORY SPECIES, Bonn Convention (CMS)

CMS aims to conserve terrestrial, aquatic and avian migratory species throughout their range. Harbour porpoise is included in Appendix II as a migratory species which has an unfavourable conservation status and which require international agreements for its conservation and management. This Appendix lists species which have a conservation status which would significantly benefit from the international cooperation that could be achieved by an international agreement.

AGREEMENT ON THE CONSERVATION OF SMALL CETACEANS OF THE BALTIC, NORTH EAST ATLANTIC, IRISH AND NORTH SEAS (ASCOBANS)

ASCOBANS was concluded in 1991 as the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS) under the auspices of the Convention on Migratory Species (CMS or Bonn Convention) and entered into force in 1994. In February 2008, an extension of the agreement area came into force which changed the name to "Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas". The Parties recognizes that by-catch, habitat deterioration and disturbance may adversely affect the population of the small cetaceans of the Baltic and North Seas; therefore they undertake to cooperate closely in order to achieve and maintain a favourable conservation status for small cetaceans. In particular, each Party should apply, within the limits of its jurisdiction and in accordance with its international obligations, conservation, research and management measures for the conservation of small cetaceans.

AGREEMENT ON THE CONSERVATION OF CETACEANS IN THE BLACK SEA, MEDITERRANEAN SEA AND CONTIGOUS ATLANTIC AREA (ACCOBAMS)

The ACCOBAMS is a cooperative tool for the conservation of marine biodiversity in the Mediterranean and Black Seas. Its purpose is to reduce threats to cetaceans in Mediterranean and Black Sea waters and improve our knowledge of these animals. In the Mediterranean Sea and Contiguous Atlantic Area the harbour porpoise (*Phocoena phcocoena phocoena*) Conservation Status is classified as “Least Concern” but *Phocoena phocoena relicta* is “Endangered” in the Northern Aegean Sea, Azov Sea, Marmara Sea and Black Sea.

CONVENTION FOR THE PROTECTION OF THE MARINE ENVIRONMENT OF THE NORTH-EAST ATLANTIC (OSPAR Convention)

The OSPAR Convention is a legal instrument guiding international cooperation between fifteen Governments of Europe and the European Union, on the protection of the marine environment of the North-East Atlantic. The new annex on biodiversity and ecosystems was adopted in 1998 to cover non-polluting human activities that can adversely affect the sea. Since the beginning OSPAR worked to identify threats to marine environment, and organised programmes and measures to ensure effective national action to combat them. Contracting Parties have to report to the OSPAR Convention what they have done to implement their obligations and commitments, and requires the OSPAR Commission to evaluate what has been achieved.

Harbour porpoise was included on the OSPAR List of threatened and/or declining species and habitats by the OSPAR Agreement 2008-6. Spain and Portugal belong to the Region IV, Bay of Biscay and Iberian Coast, where the species was considered to be one of the most common cetaceans but sightings and strandings are now only common in certain areas for example, western Galician and northern Portuguese coasts (OSPAR 2000). OSPAR is now working on the implementation of the MSFD, including development of common indicators for marine mammals.

The western Iberian Peninsula.

The West Iberian Peninsula (WIP) comprises Galicia (Northwest Spain) and Portugal. At Southern Galicia beaches cover 13.8% of the coast, but the Northern coastline is mostly rocky and shallow. The most irregular section of the WIP is Galicia, which contains many rías. The rías are flooded tectonic valleys of moderate depth. At mouths of the Rías Baixas (the rías of Vigo, Pontevedra, Arousa, Muros-Noia and Corcubión-Cee at south Galicia) there are the archipelagos of Cíes, Ons, and Sálvora. The rías form an intrinsic component of the "shelf system" (Doval et al 1998), the oceanographic characteristics of which are driven by large scale and local winds, especially during summer when freshwater input is at its minimum. To the south of Silleiro Cape, a rectilinear sandy coast extends to just north of the Nazaré Canyon, interrupted only by Cape Mondego. Further south, beaches are replaced by cliffs which extend to Cape Raso, at the latitude of Lisbon (OSPAR 2000).

The WIP is characterized by a relative narrow shelf of 20 - 35 km wide and 100 – 200 m depth, with two principal currents present: i) the Portuguese Current, a broad equatorward current, and ii) the Navidad Current (Pingree and Le Cann 1989), a branch of the Iberian Poleward Current IPC that enters the Cantabrian Sea. The area is also the northern limit of the NW African upwelling system. Upwelling on the Galician and Portuguese shelf is seasonal, occurring mainly from April to September (Figueiras et al 2002, Alvarez et al 2010), although a shorter period seems to occur on the North coast of Iberia from June to August (Alvarez et al 2010). Upwelling is caused by northerly winds during summer and Eckman transport (e.g. Fraga 1981, Figueiras et al 2002, Prego and Varela 1998). Upwelling is also associated with the IPC (Álvarez et al 2003), and the interaction of coastal upwelling and strong outflow from the rías generates eddies in the slope poleward flow, which could contribute to breakdown of the Iberian Polar Current (IPC) during the start of the upwelling regime (Torres and Barton 2007). In the North WIP, eddies are also a topographic features of the coast in areas such as the Estremadura Promontory, the Aveiro Canyon and the Porto Canyon (Peliz et al 2003). The rías form a semi-closed system because of the downwelling winds, the presence of the poleward flow and the upwelling that takes place inside them (Torres and Barton 2007).

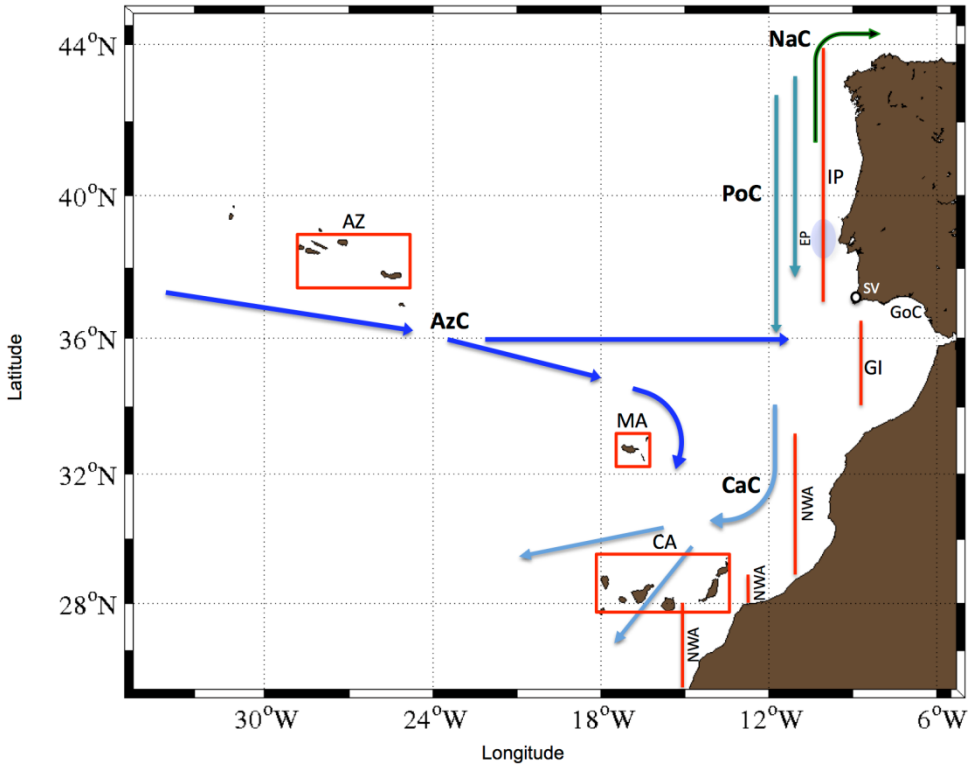


Figure 5. The main large-scale surface currents in our study area are the Azores Current (AzC), the Canary Current (CaC), and the Portugal Current (PoC). The approximate location of the Navidad Current (NaC) is also shown. Red squares delimit source/sink areas around the Macaronesian islands: Azores Archipelago (AZ), Madeira Archipelago (MA), and Canary Archipelago (CA). The red meridional lines define coastal source/sink areas: the Iberian Peninsula (IP), Northwest African coast (NWA), and Strait of Gibraltar (GI). The locations of the Gulf of Cádiz (GoC), Cape St. Vicente (SV), and Estremadura Promontory (EP) are also noted. Source: Sala et al 2013.

These oceanographic processes are important especially due to the associated enrichment of the waters, which favours biological production (e.g. Cabanas 1999, Âmbar 2002), and therefore may be good for the development and aggregation of fish and, through the food chain, for marine mammals and birds. Indeed, the WIP is a high biodiversity area with almost 400 species of fish (Bañón et al 2010) and over 75 species of cephalopods (Guerra 1992). Also, at least 22 species of cetaceans have been recorded in Galicia (Penas-Patiño and Piñeiro-Seage 1989, López el al 2003, Covelo et al 2009, 2015) and 16 species of cetaceans in Portugal (Brito et al 2009, Ferreira et al 2012), with the common dolphin (*Delphinus delphis*) the most

common species followed by bottlenose dolphin (*Tursiops truncatus*) (in Galicia) or harbour porpoise (*Phocoena phocoena*) (in Portugal).

The area's fisherys resources are used by fishermen and cetaceans and it is an area of high fishing effort (Sequeira et al 1992, EUROSTAT 2010), leading to a level of cetacean by-catch that is suspected to be unsustainably high (López et al 2012, Read et al 2012, Goetz et al 2014).

The Iberian harbour porpoise.

In the 20th century the harbour porpoise was disappearing from the Spanish Mediterranean coasts, leading to its extinction nowadays (Gaskin 1984, Blanco and Gonzalez 1992, Frantzis et al 2001). In the Cantabrian Sea its regression was evident in the last decades of that century, although it is still present (López et al 2012). Otherwise, porpoises are common in the Galician and Portuguese coasts, where they are present throughout the year, and their presence is recorded in the Gulf of Cádiz (Consejería de Medio Ambiente y Ordenación del Territorio 2015).

The Iberian population of the harbour porpoise has been defined as one of the 6 management units in European Northeast Atlantic (ICES 2014) due to genetic and morphometric studies (Sequeira 1996, López et al 2003, Rosel et al 2003, Gol'din 2004, Fontaine et al 2007 a, 2010, 2014, Viaud-Martinez et al 2007, Galatius and Gol'din 2011, Read et al 2012). Spanish and Portuguese porpoises are isolated with a gene flow from Iberia to West Africa (Tolley and Rosel 2006, Viaud-Martinez et al 2007, Fontaine et al 2012) and strong barriers to gene flow in the North with a restricted admixture zone in the Bay of Biscay (Fontaine et al 2007, 2014, Alfonsi et al 2012).

In Galician waters, harbour porpoises are most frequently observed near to the coast (López et al 2004), where the continental shelf is narrower that could indicate that they occupy deeper waters and seem to avoid bottlenose dolphins (Pierce et al 2010). In this area, bottlenose dolphin attacks on porpoises have been documented (López and Rodriguez 1995, Alonso et al 2000), although they do not appear to be frequent, it could be the reason why porpoises avoid areas frequented by bottlenose dolphins. In Portugal, the majority of sightings of porpoises were observed very near the shore. However, in some areas, the species was observed almost at the border of the continental shelf over deeper water depths (Santos et al 2012).

An estimation of the abundance in the Iberian Peninsula and the Southwest France was carried out from the large-scale survey SCANS II (Hammond et al 2013). It was calculated that there was an abundance of 2357 porpoises (CV 0.92) in the area, one of the lowest densities estimated, together with offshore west Scotland and Ireland. Other surveys were carried out to study the cetaceans of the Iberian Peninsula, thus it was possible to calculate porpoise abundance at a different scale. Then, for Galicia and Cantabrian Sea López et al (2012) estimated the abundance of harbour porpoise to be 683 individuals. Furthermore, there are abundance estimates for Galicia: 386 porpoises (López et al 2012, 2013), and, for Portugal:

1691 porpoises in 2011 which increased to 3593 in 2012, suggesting strong interannual changes in abundance. However, changes in local abundance may simply indicate changes in distribution, and regular large-scale surveys unless large-scale surveys would be needed to determine what is happening (as seen in SCANS I and II, Hammond et al 2013). In addition, rapid increases and decreases in population size are unlikely in a slow breeding mammal unless due to immigration and/or emigration.

Body length of the stranded porpoises in the Iberian Peninsula ranged from 81 - 202 cm (Read et al 2012). Females are significant bigger than males (López 2003, López et al 2012, Read et al 2012). Animals from the Cantabrian Sea were found to be smaller than Galician porpoises, especially females (Lopez et al 2012). The authors suggest that this difference could be due to the presence of more juveniles in Cantabrian waters. Porpoises of the Iberian Peninsula are larger than those from other areas of their distribution (e.g. Donovan and Bjørge 1995, Sequeira 1996, Lens 1997, Lockyer 2003, Lopez 2003, Read et al 2012, Lopez et al 2012; Table 1) supporting to be different from those of more northern populations in the East Atlántic. López (2003) estimated sexual maturity to occur at 155 cm length in males, and at 166 cm in female. A more recent study (Read et al 2012) estimated the length at sexual maturity for Iberian porpoises to be 162 cm and 185 cm for males and females respectively. Porpoises in the NWIP give birth every second year (Read et al 2012) the period of reproduction for the Iberian porpoises seems not to be much defined with a first peak in spring and a second one in summer (Barreiro et al 1994, Sequeira 1996, López 2003, López et al 2012, Silva et al 1999, Learmonth et al 2014).

Area	Females maximum length (cm)	Males maximum length (cm)	Reference
NWIP	202 (N=127)	189 (N= 136)	Read et al 2012
Atlantic Spain	202 (N= 31)	176 (N= 27)	Lens 1997
Galicia, NW Spain	202 (N= 38)	n/a	López 2003
Portugal (1981-1994)	208 (N= 22)	175 (N= 15)	Sequeira 1996
Scotland (0992-2004)	173 (N= 227)	170 (N= 252)	Learmonth 2006
British Isles (1985-1994)	189 (N= 96)	163 (N= 114)	Lockyer 1995, 2003
Ireland (2001-2003)	175 (N= 27)	157 (N= 19)	Pierce et al 2004
Denmark (1938-1998)	189	167	Lockyer and Kinze 2003
The Netherlands	160 (N= 19)	147 (N= 5)	Pierce et al 2004
France (2001-2003)	192 (N= 14)	165 (N= 17)	Pierce et al 2004
West Greenland (1988-89, 1995)	166 (N= 85)	158 (N= 91)	Lockyer et al 2003
Iceland (1991-1997)	174 (N= 474)	165 (N= 794)	Ölafsdótir et al 2003
Gulf of Maine (1989-1993)	168	157	Read and Hohn 1995

Table 1. Comparison of harbour porpoise length (edited from López et al 2012).

The main prey in the diet of porpoises in Galicia is *Trisopterus* spp, followed by blue whiting (*Micromesistius poutassou*) and *Trachurus* spp, but a total of 18 fish taxa and four cephalopod taxa were identified form stomach contents of stranded and by-catch porpoises (Read et al 2012, Pierce et al 2010). In Portugal the principal prey was the common dragonet (*Callionymus lyra*), followed by *Trisopterus* sp. and *Liza* sp. (Aguiar 2013). It was found variation in diet depending on the region, season and year of study, and body size (Aguiar 2013) as it was found in Scotland (Santos et al 2004). The study of stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) and Cd found that porpoises have a coastal foraging niche with the highest trophic position among other species such as common dolphin, long-finned pilot whale, harbour porpoise, striped dolphin and bottlenose dolphin. Bottlenose dolphins have a similar foraging niche to porpoises, but with a

lower trophic position, which suggest that they have different prey and/or they use of offshore areas (Méndez-Fernandez et al 2013).

The principal threats for the harbour porpoise in the study area are contaminants and, of especial concern, bycatch. In Galicia, the 22% of the harbour porpoises stranded are by-caught (López et al 2002). In Portugal, the 58% of the mortality is also due to by-catch, and it is related with the landings of forkbeard (*Phycis physis*), megrim (*Lepidorhombus* spp.), pargo breams nei (Pagrus spp.), sandy ray (*Leucoraja circularis*), scorpionfishes (*Scorpaena* spp.), white sea bream (*Diplodus sargus*) and blue whiting (*Micromesistus poutassou*) (Ferreira 2007). Read et al (2012) suggested that one of the reasons of that difference in the proportion of porpoises by-caught could be that gillnets are one of the gears that cause the highest rates in Galicia whereas in Portugal, although gillnets are also problematic, the beach-seines are commonly used in North-Central Portugal and are thought to be one of the gears to which harbour porpoises are most vulnerable (Sequeira and Inácio 1992, López and Valeiras 1997, López et al 2003, Ferreira 2007). For both areas, those by-catch mortality rates in strandings is very high and could be unsustainable (Ferreira 2007, López et al 2012) according to ASCOBAMS (1997), which state that an anthropogenic removal of more than 1.7% of the best available population estimate abundance represents an '*unacceptable interaction*'.

Méndez-Fernández et al (2014 a) found that harbour porpoise and bottlenose dolphin had the highest PCB concentrations among the Iberian toothed whales studied (common dolphin, long-finned pilot whale, harbour porpoise, striped dolphin and bottlenose dolphin). They were also higher concentrations than seen in those species in the Atlantic, Pacific and Indian Oceans, with the exceptions of North, Baltic and Norwegian Seas for harbour porpoise, and they are much higher than the threshold level for PCB concentrations associated with adverse health effects on marine mammals. Comparative analyses of trace element concentrations (Hg and Cd) in the same five species in the Iberian Peninsula with other studies world-wide showed that those species in that area are not specially threatened by Hg and Cd exposure. However, porpoises showed slightly higher concentrations of both elements in comparison with other areas of the Atlantic waters but far below the suggested threshold levels of effects in humans and marine mammals for renal Cd and hepatic Hg (Méndez-Fernandez et al 2014 b).

Because of the situation of the harbour porpoise in the Iberian Peninsula, it is classified as "vulnerable" in the Catálogo Nacional de Especies Amenazadas (National List of Threatened Species, Ley 4/1989, last revision R.D. 139/2011 of February 4th 2011) and in the Catálogo Gallego de Especies Amenazadas (Galician List of Threatened Species, DOG Nº 89, May 9th

2007, Annex II), which requires the elaboration of Special Management Plans for Conservation, and is protected by the Decreto Lei n.º 263/81, September 3rd in Portugal. Moreover, in both countries (Spain and Portugal) there is a transposition of the Habitat Directive of the European Union (Real decreto 1997/1995, December 7th; Decreto Lei 140/99, April 24th, and the Decreto Lei 49/2005, February 24th).

Thesis objectives.

Given that the determination of population structure and habitat preferences are among the main research needs for the adequate management and conservation of the harbour porpoise, a species of concern, and given the limited available information about porpoises in the Iberian Peninsula, this thesis will address the following objectives:

Objective 1. To determine the genetic population structure in harbour porpoise along the Northeast Atlantic and Black Sea. The spatial distribution of microsatellite and mitochondrial DNA variation was used to characterize levels of population genetic diversity and structure among putative populations from Spain (Galicia, Basque Country and Huelva), Portugal, France, Belgium, England, Scotland, Ireland and Turkey.

Objective 2. To determine the existence of genetic population structure in harbour porpoise of Iberia, and understand with more accuracy population genetic processes occurring in the area. The spatial distribution of microsatellite and mitochondrial DNA variation was used to characterize levels of regional population genetic structure among putative populations from Galicia, Basque Country and Huelva and Portugal.

Objective 3. To analyse the existence of seasonal and temporal trends in harbour porpoise distribution in Galicia from data recorded during targeted boat-surveys for cetacean studies during the years 2003-2010 carried out in Galician coastal waters. Results were compared with those of the other resident species present in the area, such as the bottlenose dolphin.

Objective 4. To determine the habitat preferences and identify suitable habitats for harbour porpoise in Galician waters from data recorded during targeted boat-surveys for cetacean studies during the years 2003-2010 carried out in Galician coastal waters. This analysis was based on the relationship between harbour porpoise presence and seven ecogeographic variables known to be important in determining the distribution of cetacean species.

Objective 5. To analyse the existence of seasonal and temporal trends in harbour porpoise distribution in Galicia from sightings recorded from land-surveys during the years 2003-2011 carried out in Galician coast. Results were compared with those of the bottlenose dolphin.

Objective 6. To determine the habitat preferences and identify suitable habitats for harbour porpoise in Galician waters from data recorded during land-surveys during the years 2003-2011. This analysis was based on the relationship between harbour porpoise presence and

eight ecogeographic variables known to be important in determining the distribution of cetacean species.

Objective 7. To detect the existence of spatiotemporal patterns and the possible presence of peaks (locations, years, months) in harbour porpoise strandings distribution in Galicia and Portugal. To determine changes in length composition and sex ratio, and proportion of porpoises by-caught.

Additional objectives include the following:

Objective 8. To assess the historical demography using mismatch distribution in the Iberian Peninsula, the North East Atlantic, the Baltic area, West Greenland, Iceland, Aegean and Marmara Sea, Black Sea and West Africa.

Objective 9. To study the validity of the proposal of the harbour porpoise upwelling ecotype (Iberian and West Africa populations) as a separate subspecies, *Phocoena phocoena meridionalis*.

Objective 10. To quantify the factors that affect the detection of harbour porpoises by observers in boat-surveys, such as boat speed, Beaufort and wind direction, Douglas, visibility, swell height, visible width and boat identity.

Objective 11. To study the factors affecting the detection of harbour porpoises by observers at land-based surveys, such as number of observers, height of the observation point, optics used, wind strength (Beaufort scale) and direction, sea state (Douglas scale), visibility, area surveyed, duration of the observation and presence of bottlenose dolphins.

Objective 12. To assess if the comparison of the distribution of harbour porpoise and bottlenose dolphin shows the avoidance of porpoises to bottlenose dolphins, for example in order to avoid aggressive interactions.

Objective 13. To quantify the effect of several variables such as year, month, location, body condition, length, sex, by-catch on length composition, sex ratio and by-catch rate of stranded animals.

Thesis outline.

This thesis consists of six main chapters, specifically written for the thesis in the format of scientific articles. Authorship of chapters for publication is shared with other researchers who have made significant contributions to the work. All co-authors are listed at the beginning of the chapters concerned.

Chapter 1 provides a general introduction to the importance of studying cetacean ecology, the biology of the harbour porpoises, the characterization of the study area, and the conservation status of harbour porpoise.

Chapter 2 examines the population structure of harbour porpoises of Northeast Atlantic and Black Sea, focusing on the porpoises of the Iberian Peninsula including samples from Spain (Galicia, Basque Country and Huelva) and Portugal, with the use of genetic markers (microsatellites and mitochondrial DNA). The genetic diversity of Iberian porpoises and genetic relationships between them and individuals form adjacent locations were investigated. Also the historical demography was studied. Moreover, the confirmation of the proposal of the harbour porpoise upwelling ecotype (Iberian and West Africa populations) as a separate subspecies, *Phocoena phocoena meridionalis*, was investigated.

Chapter 3 includes the study of the spatiotemporal trends of the harbour porpoise distribution in Galicia from data recorded during targeted boat-based surveys, the analyse of the factors that affect the detection of porpoises by observers and the identification of habitat preferences for this species along this area based on seven ecogeographic variables. Also the distribution of harbour porpoise and bottlenose dolphin was compared.

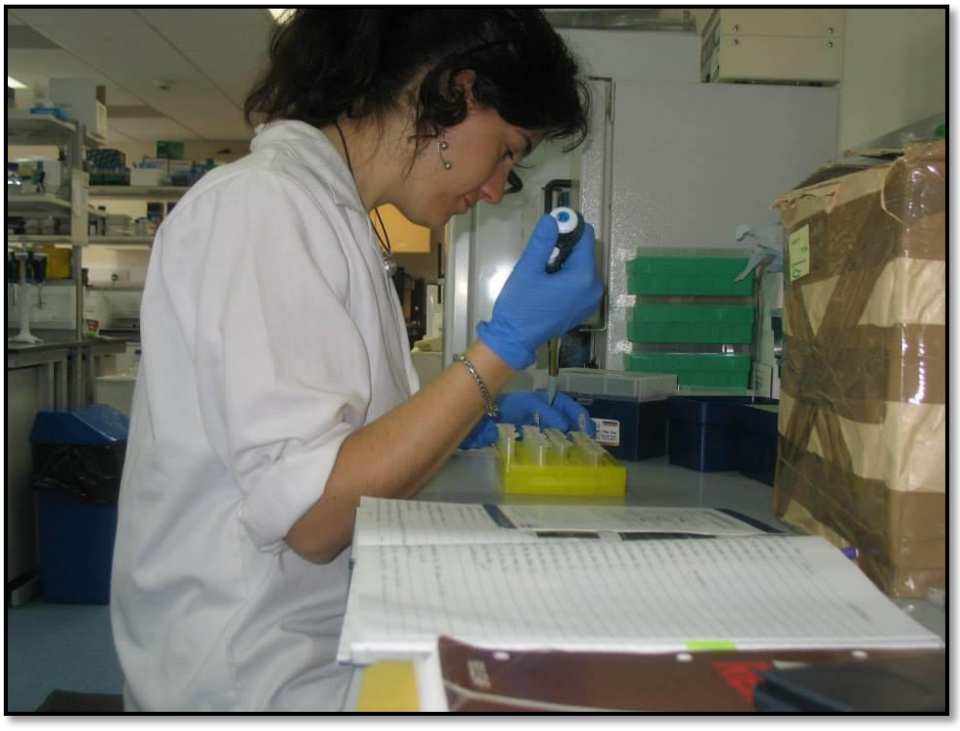
Chapter 4 includes the study of the spatiotemporal trends of the harbour porpoise distribution in Galicia from data recorded during land-based surveys, the analysis of the factors that affect the detection of porpoises by observers, and the identification of habitat preferences for porpoises along this area based on seven ecogeographic variables. Also the distribution of harbour porpoise and bottlenose dolphin was compared.

Chapter 5 studies the strandings along Galician and Portuguese coasts in order to detect the existence of spatiotemporal patterns and the possible presence of peaks of its strandings, determine changes in length composition and sex ratio, and proportion of porpoises by-caught. Additionally, the effect of year, month, location, body condition, length, sex, by-catch of stranded porpoises was quantified on length composition, sex ratio and by-catch rate.

A general discussion is provided in **Chapter 6**, which concludes and gives the perspective of this work.

CHAPTER II

Population genetic structure of harbour porpoise, *Phocoena phocoena,* from the Iberian Peninsula: evidence for population separation from NE Atlantic Ocean and Black Sea and implications for management.



Ángela LLavona, Marisa Ferreira, Pablo Covelo, Alfredo López, José V. Vingada, Graham J. Pierce, Willy Dabin, Rob Deaville, Thierry Jauniaux, Emer Rogan, Arda M. Tonay, Ayhan Dede, Andrew Brownlow, Luis Laria, Carolina Fernández, Pablo Cermeño and Stuart B. Piertney.

Conceived and designed the experiments: ÁLL and SBP.

Designed the analisys: ÁLL and SBP

Performed the experiments: ÁLL.

Analyzed the data: ÁLL.

Contributed reagents/materials/analysis tools: ÁLL, MF, PC, AL, JVV, GJP, WD, RD, TJ, ER, AMT, AD, AB, LL, CF, PC, SBP.

Wrote the paper: ALL.

Edited the text: SBP and GJP.

Provided constructive comments on the manuscript and approved the final document: SBP, GJP, AL, JVV.

Abstract

The effective definition of SACs for the harbour porpoise (*Phocoena phocoena*) requires an understanding of the species distribution and population structure.

Here population structure of the harbour porpoise in the North East Atlantic and Black Sea was examined using ten DNA microsatellite markers and sequence variation from the mitochondrial control region (*mcr*). Focus was on samples from Spain (Galicia, Basque Country and Huelva) and Portugal, which were then examined with reference to populations in France, Belgium, England, Scotland, Ireland and Turkey. Mitochondrial DNA variation in Iberian samples was also examined alongside existing data from other areas such as the North East Atlantic, the Baltic area, West Greenland, Iceland, Aegean and Marmara Sea, and West Africa, in order to obtain a wide picture of the mtDNA structure.

A Structure-based analysis of microsatellite structure identified three main genetic groups: the Iberian Peninsula, the rest of Northeast Atlantic, and the Black Sea. A median joining network of mtDNA sequences highlights the isolation of the Aegean-Marmara Sea and Black Sea populations.

Neither microsatellite nor mitochondrial DNA markers detected genetic differentiation between Galicia and Portugal, nor any significant pattern of population genetic structure along the Iberian coast. However there were differences between Iberia and the rest of the populations studied. Values of genetic diversity for both markers were lower in the Iberian Peninsula than all the other populations except those in Aegean, Marmara and Black Seas, which increases their vulnerability.

Levels of divergence clearly cannot be explained by isolation by distance but instead are likely be associated with population separation based upon oceanographic conditions due to the presence of upwelling conditions at West Iberia and North West Africa providing suitable conditions for porpoises.

Overall the genetic data suggest that the Iberian Peninsula and West Africa should be considered as a separate population, which is essential to assess threats that can affect this population, such as by-catch in commercial fisheries. It is also the basis for the creation of specific management plans and the definition of SACs as required by the EU Habitats Directive. Furthermore, this study supports the proposal to describe this population as a separate subspecies, *Phocoena phocoena meridionalis* (Fontaine et al 2014).

Introduction

To help to maintain natural habitats, populations and species as ecologically and evolutionarily viable entities with favourable conservation status, the European Union Habitats Directive mandates that Member States establish Special Areas for Conservation (SACs) for some species such as porpoises, and define robust species management plans (Council Directive 92/43/EEC). The Directive defines a “favourable" conservation status when: i) population dynamic data on the species concerned indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitat; ii) the natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future; and iii) there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis.

The effective definition of SACs and development of management plans as conservation tools require an understanding of the distribution, abundance and population structure of a species. This can be informed by a sound understanding of the spatial distribution of genetic diversity, measured through variation in allele frequencies, heterozygosity (reflecting the proportion of heterozygotes within a population), and the number of alleles per locus (representing the diversity of alleles at each locus within a population) (Lande 1988, Reed and Frankham 2003, Schwartz et al 2007). For example, if a species, which is observed in a certain geographical area, is mistakenly assumed to form a discrete population, the effect of a studied threat in that area will be over-estimated. Conversely, if a discrete population in a certain area is not recognized the effect will be underestimated (Walton 1997). This is especially important with threatened populations and particularly those which exist in degraded or fragmented habitats (Simberloff 1988, Taylor and Dizon 1999, Hanski and Gaggiotti 2004, Kraaijeveld-Smith et al 2005, Höglund 2009). When small populations become fragmented and migration between subpopulations decreases or is eliminated, the rate of loss of genetic diversity can increase through inbreeding and strong genetic drift, the probability of demographic, environmental and genetic stochasticity. This can negatively affect the long-term viability of population fragments and therefore of the entire population. Frankham et al (2002), Frankham (2005) and Garner et al (2005) found that endangered species have lower genetic diversity than non-endangered equivalents, which increases their vulnerability and consequently increases probability of extinction (Mills and Smouse 1994, Lacy 1997, Frankham et al 2002, Frankham 2005). In contrast, populations with frequent dispersal and gene flow can deal those stochastic/ecological effects and

decrease extinction risk (Lande 1998, Tallmon et al 2004, Pérez et al 2009). As such, assays of the levels of genetic diversity within properly defined population boundaries in natural populations can inform on the risk of population extinction, gauge longer term population viability and measure the success of conservation efforts.

Neutral genetic markers such as microsatellite DNA length polymorphisms and mitochondrial DNA sequence variants have been extremely effective in determining population structure and identifying populations with reduced diversity (Brunner et al 1998, Hoelzel et al 2002, Johnson et al 2003, Epps et al 2005). The spatial distribution of diversity at these markers is affected only by gene flow and drift, so they in essence measure dispersal or conversely population isolation. They have been used for conservation purposes both in terrestrial species such as the red grouse (*Lagopus lagopus scoticus*; e.g. Piertney et al 1998, 2000), the European red-billed chough (*Pyrrhocorax pyrrhocorax*; e.g. Wenzel et al 2012), the European brown bear (*Ursus arctos*; e.g. Swenson et al 2011, Kocijan et al 2011, FAPAS 2013) and the Iberian lynx (*Lynx pardinus*; e.g. Delibes et al 2000, Johnson et al 2004); and marine species such as the seahorse (e.g. Teske et al 2003, Thangaraj et al 2012, Nickel and Cursons 2012), the abyssal grenadier (*Coryphaenoides armatus*; Ritchie et al 2013), the bluefin tuna (*Thunnus thynnus*; Carlsson et al 2004, Ferrara et al 2010, Riccioni et al 2010, 2013, Cannas et al 2012), and the common guillemot (*Uria aalge*; e.g. Riffault et al 2005, Morris-Pocock et al 2008). Moreover, microsatellites represent a useful proxy for overall genomic diversity given that heterozygosity of neutral markers is expected to be positively correlated with that of loci under selection (Hansson and Westerberg 2002, Reed and Frankham 2003) and as such reductions in microsatellite diversity can identify genetically eroded populations.

Mitochondrial DNA (mtDNA) can provide insight into contemporary ecological processes acting on a population, such as sex-biased dispersal through the spatial distribution of haplotypes in a landscape, but can also provide a historical perspective in a phylogeographic context. Thus, differences in haplotype frequencies may be reflective of more contemporary population structure, while phylogeographic structure will often reflect historical patterns in population structure (Moritz 1994) associated with historic geological events such as tectonic movement of landmasses, floods or glaciation (Taberlet et al 1998, Hewitt 2000). The use of both mitochondrial and microsatellite markers in concert provides a recent and an historic perspective on the processes influencing genetic structure and diversity.

The harbour porpoise (*Phocoena phocoena*) is a small cetacean present in the North Atlantic, North Pacific, and the Black Sea (Gaskin 1984). It is primarily restricted to coastal and

continental shelf waters but is occasionally observed in the deep oceanic waters between major land masses (Donovan and Bjørge 1995, Read and Westgate 1997, NAMMCO 1998, Teilmann and Dietz 1998, Skove et al 2003, Sveegaard et al 2015). It is included in Annex-II of the EU Habitats Directive and as such, the designation of SACs is a priority issue. The IWC (International Whaling Commission) and ICES (International Council for the Exploration of the Sea) recommended studies to determine the broad scale population structure of porpoises to develop an appropriate management plan, in order to reduce negative impacts on the populations. Despite being the most common cetacean species in the North Atlantic (Hammond et al 2002, 2013), it is very sensitive to anthropogenic disturbance and several important threats have been described for the species, such as pollutants (e.g. Bennet et al 2001, Das et al 2004 b, Mahfouz et al 2014 a, b), climate change (e.g. Learmonth et al 2006, MacLeod 2009, Heide-Jørgensen et al 2011), prey abundance (e.g. MacLeod et al 2007), noise (e.g. Madsen et al 2006, Tougaard et al 2009, Teilmann and Castensen 2012) and fishery by-catch (e.g. IWC 1994, Donovan and Bjørge 1995, ASCOBANS 2000). By-catch is especially important given that, in many areas, the incidental by-catch estimates exceed the limit of mortality considered as acceptable by ASCOBANS (1997), namely 1.7% of the population annually (e.g. Ferreira 2007, Bjørge et al 2012, López et al 2012, Goetz et al 2014, ICES 2014). The distribution of porpoises in the eastern Atlantic is essentially continuous, although genetic differentiation between individuals has been observed to increase with geographic distance (Fontaine et al 2007, Tolley and Rosel 2006). Although the reasons are not well understood, there is an obvious and ongoing return of harbour porpoises along Dutch (Camphuysen 2004), German (Thompsen et al 2006, Siebert et al 2006), Southwest British (Pikesley et al 2011), Belgian (Jauniaux et al 2002) and French coasts (Jauniaux et al 2002, Jung et al 2009) where in the near past they have been reduced or disappeared. Moreover, marked differences in the distribution between 1994 and 2005 were reported, with centres of higher densities in northern areas of the North Sea in 1994 having shifted southwards by 2005 (Hammond et al 2013).

Porpoise have been absent from the Mediterranean for the past few centuries, if not the last few millennia (Frantzis et al 2001, Fontaine et al 2010). Some recent observations of individuals have been made in the northern Aegean (Frantzis et al 2001), but these appear to be Black Sea individuals that have entered the region (Rosel et al 2003).

Habitat discontinuities, changes in oceanographic features, prey distribution and philopatric behaviour have been identified as influencing the spatial genetic structure of several delphinid

species (e.g. Hoelzel et al 1998, Fullard et al 2000, Natoli et al 2005, Bilgmann et al 2007, 2008, Möller et al 2007, 2011, Rosel et al 2009, Mendez et al 2010, 2011, Amaral et al 2012 a, b, Ansmann et al 2012, Gaspari et al 2013, Richards et al 2013). It is considered that there are three processes that have influenced the distribution of genetic diversity across extant porpoise populations in North East Atlantic. 1) Historical isolation, such as is seen with the Black Sea, that may have taken place when the Mediterranean Sea became warm and oligotrophic after the Last Glacial Maximum, causing the fragmentation and retreating of the species in that region (Tolley and Rosel 2006, Fontaine et al 2010); 2) environmental conditions such as upwelling that affect water temperature and increase the productivity of an area (e.g. Fraga 1981, Figueiras et al 2002). Such effects are considered to influence porpoise abundance and distribution around Iberia and North West Africa (Fontaine et al 2007, 2014, Alfonsi et al 2012, Chapters III and IV); and 3) shifts in distribution and movement and isolation of populations on the continental shelf due to philopatry, foraging specialization or seasonal migration (Tiedemann et al 1996, Andersen et al 1997, 2001, Walton 1997, Rosel et al 1999 a, Fontaine et al 2007, Wiemann et al 2010, Alfonsi et al 2012, de Luna et al 2012).

The genetic population structure of harbour porpoises in the North Atlantic has been studied previously using allozyme electrophoresis (Andersen 1993), microsatellites DNA (Andersen et al 1997, Andersen et al 2001, De Luna et al 2012, Fontaine et al 2007, 2010); RFLP analysis of mitochondrial DNA (Wang et al 1996, Wang and Berggren 1997); mitochondrial DNA sequencing (Rosel et al 1995, 1999 a, 2003, Tiedemann et al 1996, Tolley et al 1999, 2001, Walton 1997, Tolley and Rosel 2006, Viaud-Martinez et al 2007, Tonay et al 2012); or a combination of markers (Rosel et al 1999 b, Wiemann et al 2010, Alfonsi et al 2012, Fontaine et al 2014). These studies have together confirmed the genetic isolation of the Black Sea population and the absence of a clear population structure across the European continental shelf, considering structuring to be weak from the northern Bay of Biscay to Norway and Iceland (Andersen et al 2001, Tolley and Rosel 2006, Fontaine et al 2007, Wiemann et al 2010, Alfonsi et al 2012).

Several of these studies have included samples from the Iberian Peninsula. Tolley and Rosel (2006) analysed samples from Portugal and suggested that there is limited gene flow between Europe and West Africa, thus the latter should be considered a separate population. They also found that porpoises from the Black Sea were divergent to those from West Africa and Portugal, which was corroborated by Viaud-Martinez et al (2007), who analysed samples from the area of Gibraltar and found that they were more closed related with French porpoises than

with Black Sea animals, but highlighted the need for more samples from Portugal and Mauritania to assess if Gibraltar porpoises were part of the African population.

Fontaine et al (2007) found that porpoises from Spain and Portugal were a genetically homogeneous group that had much lower genetic diversity than that observed in the North Atlantic but similar to genetic diversity in the Black Sea. Strong barriers to gene flow in the southern Bay of Biscay were detected, which isolated, at a relatively small scale, porpoises from Iberian waters. This isolation was estimated to occur only approximately 300 years ago with a predominant northward migration, contemporaneous with the warming trend underway since the 'Little Ice Age' period, and with the ongoing retreat of cold-water fishes from the Bay of Biscay (Fontaine et al 2010).

More recently, Fontaine et al (2014) defined three ecotypes of harbour porpoises as a consequence of a divergence event during the Last Glacial Maximum: Black Sea, upwelling (Iberia and Mauritania) and European continental shelf waters ecotypes (from northern Bay of Biscay to Norway). Their analyses also suggest that Iberian and Mauritanian porpoises are likely descended from the extinct populations that once inhabited the Mediterranean during the glacial and post-glacial period.

There has been asymmetrical gene flow detected between Iberia to France, and therefore these two previously separated populations of harbour porpoises are now admixing (Alfonsi et al 2012, Fontiane et al 2014). Moreover, some gene flow from Iberia to Mauritania was detected but not in the reverse direction (Fontaine et al 2014); therefore the Iberian population could be acting as a source population.

These studies have the limitation of small sample sizes for Iberian populations and thus they may not represent the definitive pattern of genetic structure in this region. This study focuses on Iberian porpoises and uses a larger number of samples to provide a higher resolution and understand with more accuracy population genetic processes occurring in the area. Using a large-scale analysis of genetic, phylogeographic structure and diversity it will be possible to robustly describe the relationship between Iberian porpoises and those from North East Atlantic and Black sea, as well as characterise any substructure or philopatry along the Iberian coast to confirm the existence of a putative upwelling ecotype.

All this information will help to increase the knowledge about harbour porpoises of Iberian waters and to correctly interpret the information from other studies using non-molecular

approaches (e.g. sightings, strandings, acoustics), to assess the threats that affect the population, and establish SACs and management strategies to maintain long-term viability of this population as is required by the EU Habitats Directive.

Materials and methods

Sample collection.

Skin, muscle and/or kidney samples were obtained from a total of 336 stranded and by-caught harbour porpoises from eight geographical locations: Spain (SP, *N*=65), Portugal (PT, *N*=124), France (FRA, *N*=24), Belgium (BEL, *N*=34), England (ENG, *N*=24), Scotland (SCO, *N*=25), Ireland (IRE, *N*=24) and Turkey (TUR, *N*=16). Samples from Spain can be regionally separated into the Basque Country (BCO, *N*=2), Galicia (GAL, *N*=61) and Huelva (HUEL, *N*=2). Samples were preserved in 96% ethanol with subsequent storage at ambient temperature; or 20% dimethyl sulfoxide (DMSO) solution saturated in NaCl with storage at -20°C; or frozen at -20°C.

DNA was extracted using the DNeasy Blood and tissue kit (Qiagen Ltd) according to manufacturer's instructions using 3 mm^3 of tissue, with elution into 200 µl of buffer AE.

Microsatellite genotyping.

Individuals were genotyped at ten microsatellite loci: Igf-I (Kirkpatrick 1992, Andersen et al 1997), 415/416 (Amos et al 1993, Andersen et al 1997), GT015 (Amos et al 1993, Andersen et al 2001), EV94 (Valsecchi and Amos 1996), PPH110, PPH104, PPH130, PPH137 (Rosel et al 1999 b), GT011 (Bérubé et al 1998) and GATA053 (Palsbøll et al 1997). Primer sequences are provided in Table 2.

PCRs were carried out in a 10µl volume containing 10 - 15 ng of DNA, 0.2 mM dNTP's, 5 pmol of each primer and 0.5 units of *Taq* polymerase (Bioline Ltd). Overall $MgCl_2$ concentrations are given at Table 2. For loci Igf-I, EV94, PPH110, GT011 and PPH130 PCR temperature profiles had an initial denaturation step of 2 min at 95°C, followed by 20 TouchDown cycles from 60 to 50°C in 0.5°C decrements (denaturation at 92°C for 30 s, annealing for 1 min, elongation at 72°C for 30 s). The programme was completed with 20 standard cycles of denaturation at 92°C for 30 s, annealing at 50°C for 30 s, elongation at 72°C for 30 s with a final elongation step at 72°C for 2 min. For PPH104 the TouchDown profile was from 65 to 55°C in 0.5°C decrements and the programme was completed with 18 standard cycles (denaturation at 94°C for 30 s, annealing at 55°C for 30 s, elongation at 72°C for 30 s). GATA053 was amplified following a 10 TouchDown cycles from 60 to 65°C in 0.5°C decrements (denaturation at 94°C for 30 s, annealing for 1 min, elongation at 72°C for 1 min). The programme was completed with 20 standard cycles (denaturation at 94°C for 30 s, annealing at 60°C for 30 s, elongation

at 72°C for 1 min) and a final elongation step at 72°C for 2 min. 415/416, GT015 and PPH137 was amplified following Fontaine et al 2006.

Forward primers were labelled with 6-FAM, HEX or NED fluorescent labels (Table 2). The PCR products from three different PCRs involving different fluorescent labels were mixed in equal volumes, diluted 1 in 10 then genotyped on an automatic ABI 3730 capillary DNA sequencer (Sequencing Service, University of Dundee, UK).

Microsatellite analysis.

Genotypes were scored by eye using the software GENEMARKER 1.4 (SoftGenetics 2010).

The absence of null alleles and large allele dropout was confirmed using MICROCHECKER 2.2.3. (van Oosterhout et al 2004). Genetic diversity was assessed by the number of alleles, number of private alleles and allelic richness using the software FSTAT2.9.3.2 (Goudet 1995, 2002). The software STRUCTURE2.2. (Pritchard et al 2000) was used to determine the most probable number of putative populations (K) that best explained the pattern of genetic variability. The number of assumed genetic clusters (K) was set from 1 to 10 due to the different geographical origin of the samples and 10 runs were performed for each K with burn-in of 10,000 and 50,000 simulations using the admixture ancestry model with correlated allele frequencies. STRUCTURE HARVESTER 0.6.7 (Earl 2011) was used to collate the results and infer the statistically best supported K using the DK statistic (Evanno et al 2005). Replicate runs for each K were aligned and averaged in CLUMPP1.1.2 (Jakobsson and Rosenberg 2007), using the *Greedy* alignment algorithm with 10 randomised input orders, and visualised using DISTRUCT1.1 (Rosenberg 2004).

In order to visualize the genetic relationship among individuals belonging to the different geographic regions, factorial correspondence analyses (FCA) were carried out using the Genetix 4.05 program (Belkhir et al 1996-2004).

Global and pairwise genetic differentiation among ten populations using Structure were estimated using the statistics D (Jost 2008) and F_{ST} (Wright 1951). The software SPADE (Chao and Shen 2010) was used to calculate an adjusted estimator for global and pairwise D (D_{est}) with 95% confidence intervals (CI) constructed from 1000 bootstrap replicates using a percentile method and re-centering (Chao and Shen 2010). F_{ST} estimates (Weir and Cockerham 1984) were calculated in FSTAT2.9.3.2 (Goudet 1995, 2002).

Population differentiation was also tested using a hierarchical analysis of molecular variance (AMOVA) in ARLEQUIN 3.5.1.2 (Excoffier and Lischer 2010) that partitions genetic variation among groups as defined from the Structure analysis, within groups and among populations, and within populations.

Observed (H_o) and expected (H_e) heterozygosities were calculated at each locus and for each population, and deviations from the Hardy–Weinberg equilibrium were tested using the Markov chain method (chain length: 1000000, dememorization steps: 100000) with ARLEQUIN 3.5.1.2. For each population, the overall deviation from the Hardy–Weinberg equilibrium was estimated based on F_{IS} values (10000 randomisations) using the software FSTAT 2.9.3.

Mitochondrial DNA sequencing.

Three different regions of the mtDNA were sequenced: Control Region (*mcr*), ATPase 6 and 8 (ATP), and NADH dehydrogenase 5 (ND5) (Table 6). For *mcr* a 488 bp fragment was amplified using the primers mcrf and mcrr, derived from L15928 and HOOO34 (Rosel et al 1995, Kocher et al 1989). For ATP a 1061 bp fragment and for ND5 a 1007 pb fragment were amplified using the primers used by Fontaine et al (2014) (Table 5). All PCR reactions were carried out in a 50 µl final volume containing 10 - 15 ng of DNA, 0.2 mM dNTPs, 5 pmol of each primer, 2.5 mM MgCl2 and 0.1 units of Taq polymerase (Bioline Ltd). Cycling parameters for the *mcr* amplification were: an initial denaturation step at 95°C for 2 min followed by 5 cycles of 95°C for 30 s, 46°C for 30 s and 72°C for 60 s each, followed by 35 cycles consisting 95°C for 30 s, 53°C for 30 s and 72°C for 60 s. Reactions were ended by a final extension step of 10 min at 72°C (Alfonsi et al 2010). For ATP and ND5 an initial denaturation step at 95°C for 2 min was followed by 35 cycle of denaturation at 95°C for 1 min, primers hybridization at the gene specific annealing temperature (T_a) provided in the Table 5 for 1 min, and an elongation step at 72°C for 1.5 min, with a final elongation step at 72°C for 30 min (Fontaine et al 2014). PCR products were purified using the QIAquick PCR Purification Kit (QIAGEN) according to the manufacturer's instructions and diluted to 2ng ul^{-1}. Using the same forward primers as were used in the original PCR, DNA sequencing was performed by Eurofins MWG GmbH, Ebersberg, Germany.

All sequences were checked by eye and aligned using MEGA 4.0 (Tamura et al 2007). Sequences were confirmed as mitochondrial control region, ATP and ND5 sequences by National Center for Biotechnology Information (NCBI) BLAST comparison. Novel haplotypes were deposited in GENBANK under accession numbers KM233834, KM233835 and KM233836.

A median-joining network was constructed for each locus using the program NETWORK 4.6.1.1 (Bandelt et al 1999).

Population differentiation was estimated as F_{ST}, using the program ARLEQUIN 3.5.1.2., and as Dxy, using DnaSP version 5.10 (Librado and Rozas 2009). Haplotype diversity (Hd) and nucleotide diversity (π) were estimated using ARLEQUIN 3.5.1.2.

Historical demography was assessed using mismatch distribution. Observed and expected numbers of pairwise nucleotide differences under a model of sudden expansion were calculated for every sampling area using DnaSP version 5.10 and Arlequin version 3.5.1.2. The fit of observed and expected distribution was tested using Harpending's raggedness index (r; Harpending 1994).

To quantify the genetic divergence between samples an Analysis of Molecular Variance (AMOVA) was undertaken using ARLEQUIN 3.5.1.2., apportioning variance among groups as defined by the Structure analysis, within groups and among populations and within populations.

Results

Microsatellites.

In total, 310 individuals (59 from Galicia, 2 from the Basque Country, 2 from Huelva, 118 from Portugal, 24 from France, 16 from Belgium, 24 from England, 25 from Scotland, 24 from Ireland and 16 from Turkey; Fig.6) were genotyped at 10 microsatellite loci. The number of alleles per microsatellite locus ranged from nine (loci GATA053) to 24 (loci GT015) (Table 2).

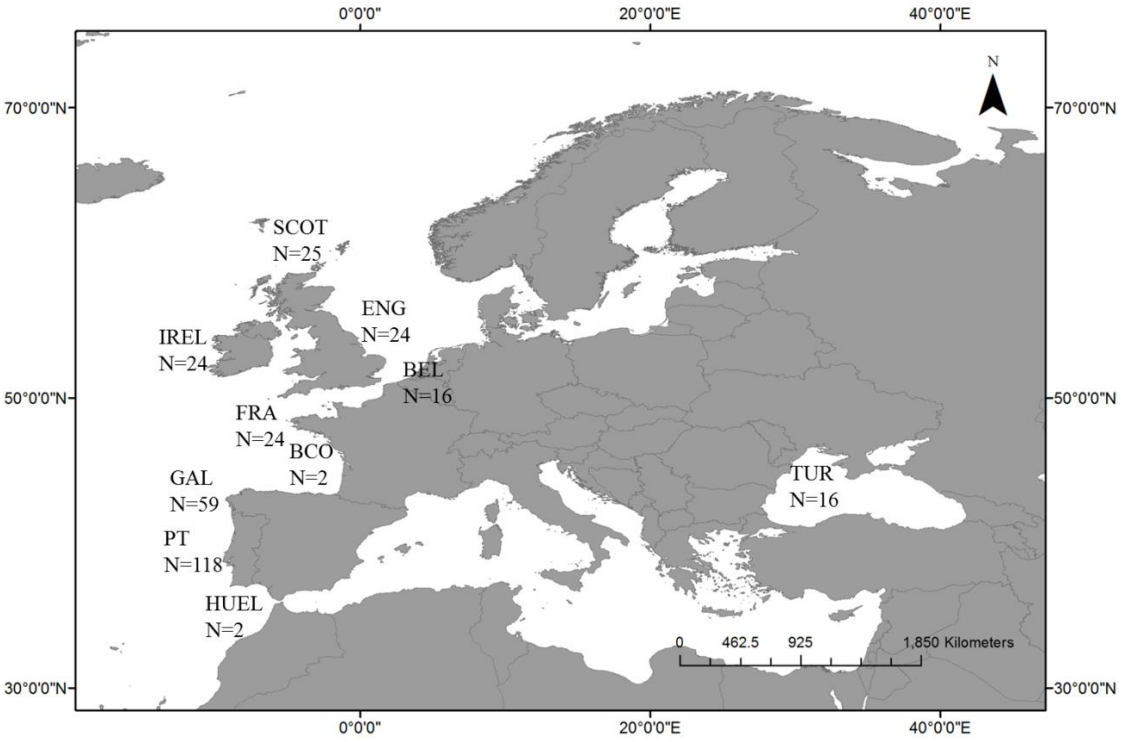


Figure 6. Sampling locations and sizes for harbour porpoise (*Phocoena phocoena*) for microsatellite analyses; GAL Galicia, BCO Basque Country, HUEL Huelva, PT Portugal, FRA France, BELG Belgium, IREL Ireland, ENG England, SCOT Scotland, TUR Turkey.

Locus name	Primer sequence	Ta (°C)	Mg2+ (mM)	Size range (bp)	Na
Igf-I [a, b]	6FAM-GGGTATTGCTAGCCAGCTGGT CATATTTTTCTGCATAACTTGAACCT	TD 60 → 50	2,5	127-153	15
415/416 [c]	NED-GAGAATGGCTGGGCTCAGATC TTCCCTATTAGAGGCTCACGA	TD 50 → 41	2,5	205-283	10
GT015 [d, e]	NED-GAGAATGGCTGGGCTCAGATC TTCCCTATTAGAGGCTCACGA	58°C	2,5	120-172	24
EV94 [f]	6FAM-ATCGTATTGGTCCTTTTCTGC AATAGATAGTGATGATGATTCACACC	TD 60 → 50	1,5	184-206	10
PPH110 [g]	HEX-ATGAGATAAAATTGCATAGA ATCATTAACTGGACTGTAGACCTT	TD 60 → 50	2,5	99-125	11
PPH104 [g]	HEX-CCTGAGGTGTGTAGTCA GACCACTCCTTATTTATGG	TD 65 → 55	2,5	142-188	18
GT011 [h]	NED-CATTTTGGGTTGGATCATTC GTGGAGACCAGGGATATTG	TD 60 → 50	2,5	96-132	14
PPH130 [g]	NED-CAAGCCCTTACACATATG TATTGAGTAAAAGCAATTTTG	TD 60 → 50	2,5	158-198	16
PPH137 [g]	6FAM-CAGGGCGGCCATGTACAGTTGAT GAGTTTGGCTCCCTCTCCAG	58°C	1,5	98 - 122	13
GATA053 [i]	6FAM-ATTGGCAGTGGCAGGAGACCC GACACAGAGATGTAGAAGGAG	TD 65 → 60	2,5	247-271	9

Table 2. Characterisation of 10 microsatellite loci for harbour porpoise. Ta, annealing temperature; Na, number of alleles.TD, Touch Down annealing temperature gradient. [a] Kirkpatrick 1992, [b] Andersen et al 1997, [c] Sclöetterer et al 1991, [d] Amos et al 1993, [e] Andersen et al 2001, [f] Valsecchi & Amos 1996, [g] Rosel et al 1999 b, [h] Bérubé et al 1998, [i] Palsbøll et al 1997.

MICROCHECKER analyses showed the possible presence of null alleles at loci GT015 and GATA053, from heterozygote deficiencies. However, as this was not consistent across populations for any locus, it was considered that this was not due to null alleles.

The best supported number of *a posteriori* genetic clusters for STRUCTURE analyses based on ΔK statistic was K=2 for the standard admixture model (ΔK= 97; Fig.7). One group comprised Galicia, Basque Country, Huelva and Portugal, and the other one the rest of the populations (Fig.8). The second best supported number of groups was K=3 (ΔK= 22) which divided the samples in one group for Galicia, Basque Country, Huelva and Portugal, a second group for the rest of Europe and a third group for Turkey.

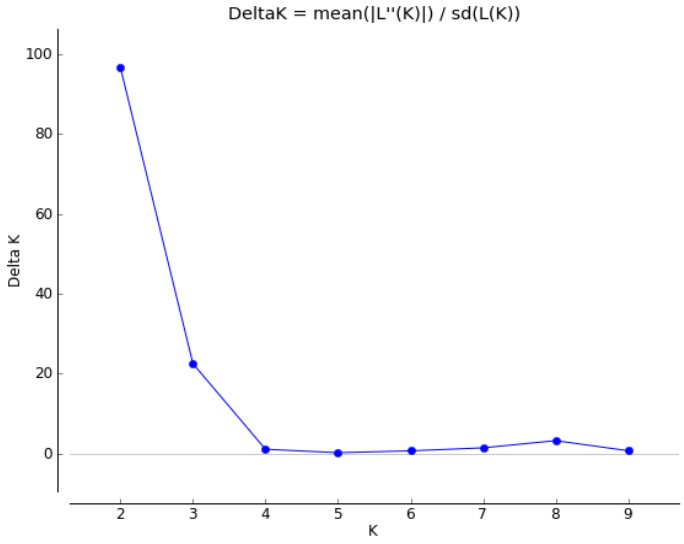


Figure 7. Results of STRUCTURE analysis, showing mean probabilities of the data (LnPr(x|k)) based on 10 STRUCTURE replicated runs plotted as a function of the putative number of clusters (K).

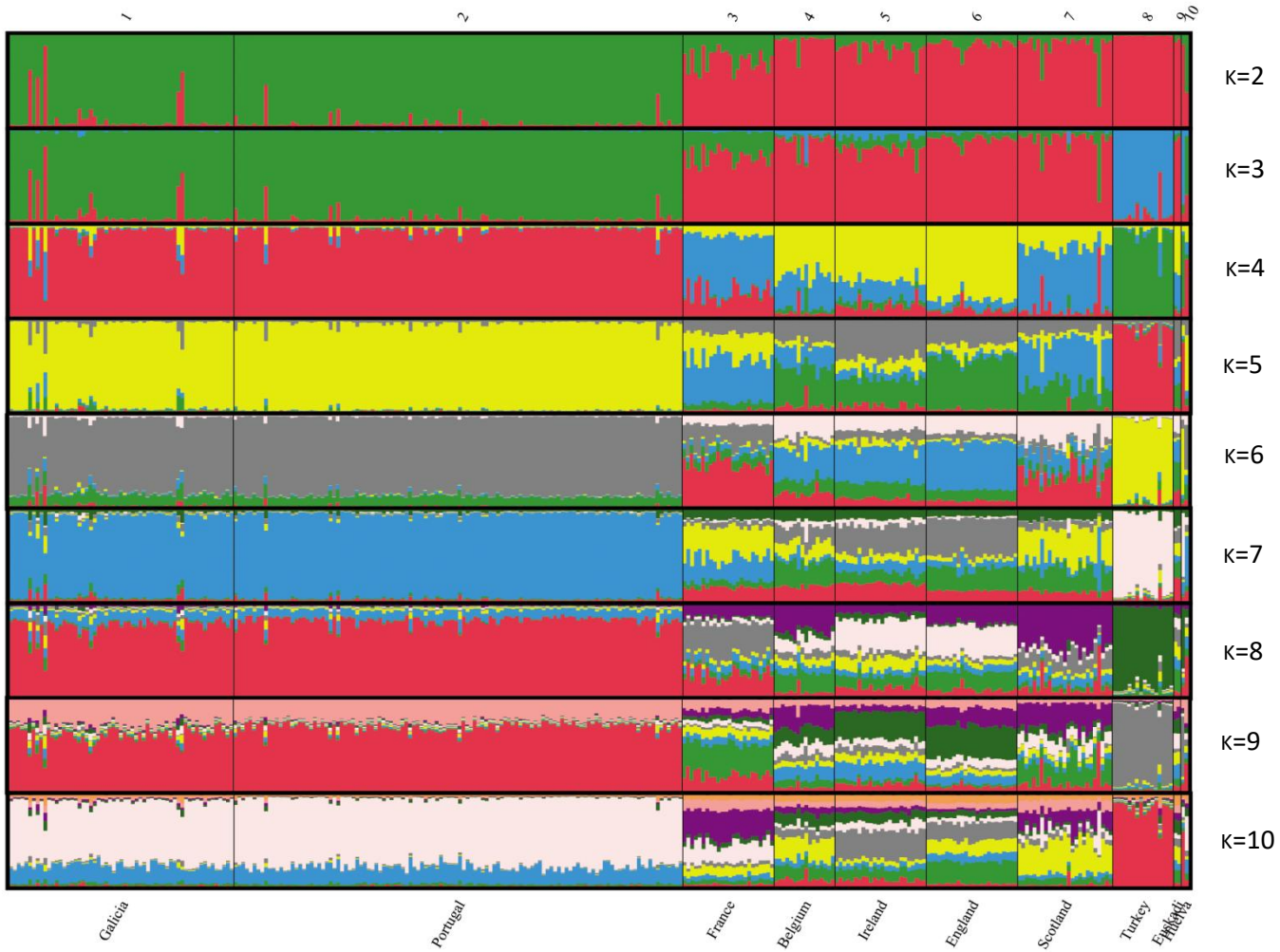


Figure 8. Estimated proportions of the coefficient of admixture of each individual's genome that originated from population K, for K= 2 to 10. Each individual is represented by a column.

The FCA analysis confirmed a level of population structure among samples (Fig.9). Analyses show three groups: 1) Spain and Portugal, 2) rest of Europe, and 3) Black Sea; with the two first principal coordinates explaining 52.19% of the variation.

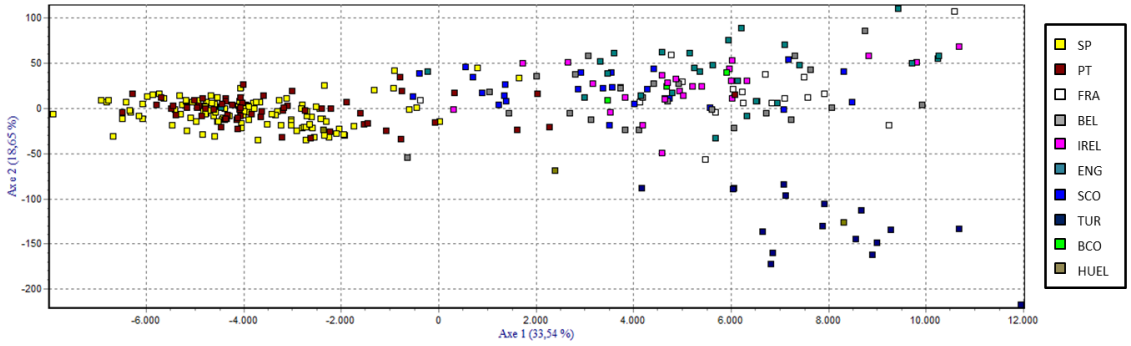


Figure 9. Principal coordinates analysis, PCoA, based on genetic distances between individuals, showing main patterns of data variation over 10 loci: 52.19% of the variability explained by principal coordinates 1 and 2. Population names as in Fig. 6.

Pairwise genetic differentiation among the 10 populations and using k=3 were calculated as F_{ST} and D_{est} (Table 3). Differences between Galicia and Portugal for F_{ST} were not significant, but were significant to the other locations except for Huelva and Basque Country, although the low number of samples for those areas has to be kept in mind. Turkey was also significantly different to the rest of the populations excepting Huelva and Basque Country; this differentiation was greater with Spain and Portugal than with the rest of Europe, supporting the Structure results for k=3. Huelva and Basque Country were not different to any other population. France, Belgium, Ireland, Scotland and England were only significantly different to Spain, Portugal and Turkey.

The D_{est} estimate was also not significant for Galicia versus Portugal, and Huelva versus the rest of populations. France, Belgium, Ireland, England, Scotland and Basque Country only showed significant differences with Galicia, Portugal and Turkey.

For K=3 all F_{ST} and D_{est} estimates were significant (Table 3b).

Population	N	PORT	GAL	FRA	BELG	IREL	ENG
N		118	59	24	16	24	24
PORT	118	-	-0.001 (0.000, 0.015)	0.091 (0.040, 0.152)	0.169 (0.095, 0.240)	0.134 (0.077, 0.194)	0.177 (0.119, 0.242)
GAL	59	0.0039	-	0.105 (0.058, 0.159)	0.190 (0.120, 0.259)	0.142 (0.090, 0.201)	0.199 (0.145, 0.256)
FRA	24	0.0431***	0.0510***	-	0.021 (0.000, 0.104)	0.003 (0.000, 0.062)	0.042 (0.000, 0.109)
BELG	16	0.0789***	0.0909***	0.0097	-	-0.001 (0.000, 0.072)	-0.024 (0.000, 0.047)
IREL	24	0.0621	0.0686***	0.0028	0.0076	-	-0.001 (0.000, 0.053)
ENG	24	0.0839***	0.0959***	0.0159	-0.0012	0.0066	-
SCOT	25	0.0945***	0.0996***	0.0129	0.0138	0.0209	0.0124
TUR	16	0.2119***	0.2120***	0.1145***	0.1207	0.0947	0.1166***
BCO	2	0.1620	0.1816***	0.0591	0.0558	0.0590	0.0683
HUEL	2	0.0350	0.0510	-0.0174	-0.0030	-0.0135	0.0007

Population	N	SCOT	TUR	BCO	HUEL
N		25	16	2	2
PORT	118	0.215 (0.152, 0.275)	0.404 (0.329, 0.485)	0.261 (0.087, 0.440)	-0.014 (0.000, 0.184)
GAL	59	0.219 (0.165, 0.275)	0.398 (0.325, 0.467)	0.296 (0.134, 0.454)	-0.003 (0.000, 0.190)
FRA	24	0.025 (0.000, 0.087)	0.260 (0.180, 0.346)	0.127 (0.000, 0.320)	-0.096 (0.000, 0.101)
BELG	16	0.014 (0.000, 0.085)	0.228 (0.136, 0.339)	0.067 (0.000, 0.299)	-0.022 (0.000, 0.237)
IREL	24	0.050 (0.000, 0.119)	0.207 (0.120, 0.299)	0.114 (0.000, 0.330)	-0.067 (0.000, 0.147)
ENG	24	0.024 (0.000, 0.080)	0.264 (0.182, 0.351)	0.115 (0.000, 0.332)	-0.011 (0.000, 0.227)
SCOT	25	-	0.297 (0.215, 0.390)	0.210 (0.000, 0.408)	0.061 (0.000, 0.284)
TUR	16	0.1279	-	0.264 (0.069, 0.462)	0.049 (0.000, 0.280)
BCO	2	0.0674	0.1967	-	0.218 (0.000, 0.478)
HUEL	2	0.0291	0.0841	0.0693	-

Table 3. Estimates of population differentiation expressed as FST (below diagonal) and Dest (above diagonal) based on microsatellite length polymorphism for a) 10 populations where significance indicated at strict Bonferroni-corrected level (α=0.00111). N: sample sizes. Population names as in Fig. 6.

Population	N	Group 1	Group 2	Group 3
N		181	113	16
Group 1	181	-	0.157 (0.128, 0.186)	0.394 (0.327, 0.466)
Group 2	113	0.0655***	-	0.250 (0.186, 0.318)
Group 3	16	0.2046***	0.0987***	-

Table 3. b) k=3, where significance indicated at strict Bonferroni-corrected level (α=0.01667***). N: sample sizes. Population names as in Fig. 6.

Analyses of molecular variance (AMOVA) revealed significant divergence among populations (Table 4). Most genetic variation occurred within populations (89.93%). The second largest variance component was attributed to divergence among groups (9.10%), while the smallest fraction of the variance was due to divergence among populations within groups (0.97%).

Regions	Degrees of freedom	Sum of squares	Variance components	P-value	Percentage of variation
Among groups	2	42.295	0.11823	0.00098+-0.00098	9.10
Within groups among populations	7	12.569	0.01262	0.00293+-0.00164	0.97
Within populations	608	710.330	116.831	0.00000+-0.00000	89.93

Table 4. Analyses of molecular variance (AMOVA) for microsatellite data.

Allele frequencies for populations and k=3 are shown in Appendix I. Galicia was the population with the most private alleles and none were found for Portugal or Basque Country, but in the latter case it could be due to small sample size (Fig. 5). Allelic richness was highest in Ireland and smallest in Turkey. For K=3, Group 2 (rest of Europe) had the highest number of private alleles and highest allelic richness, while Group 3 (Turkey) had only one private allele and the lowest allelic richness.

Significant deviations from Hardy–Weinberg equilibrium (α =0.05) based on F_{IS} estimates were found for loci Igf-1 and GT015 for the Scottish putative population. For the Structure-derived k=3 grouping, deviations were found in loci GT015 and GATA053 for Group 2.

	PORT	GAL	FRA	BELG	IREL	ENG	SCOT	TUR
N	118	59	24	16	24	24	25	16
Private alleles	0	6	4	1	3	4	2	1
Average±SD								
N alleles	9.200 ± 4.962	9.000 ± 4.922	8.600 ± 3.307	7.900 ± 3.348	9.100 ± 3.213	9.100 ± 4.149	9.000 ± 4.346	4.800 ± 1.398
Allelic richness	1.610 ± 0.214	1.610 ± 0.203	1.762 ± 0.176	1.754 ± 0.259	1.768 ± 0.171	1.761 ± 0.238	1.767 ± 0.216	1.549 ± 0.182
Ho	0.585 ± 0.209	0.590 ± 0.216	0.688 ± 0.198	0.769 ± 0.307	0.759 ± 0.273	0.761 ± 0.296	0.662 ± 0.227	0.524 ± 0.231
He	0.610 ± 0.203	0.620 ± 0.214	0.763 ± 0.172	0.754 ± 0.259	0.768 ± 0.170	0.761 ± 0.238	0.767 ± 0.216	0.549 ± 0.182
F_{is}	0.048	0.041	0.095	-0.021	0.012	0.001	0.139***	0.047

	BCO	HUEL
N	2	2
Private alleles	0	1
Average±SD		
Nalleles	2.778 ± 0.667	2.556 ± 0.882
Allelic richness	1.717 ± 0.273	1.717 ± 0.324
Ho	0.778 ± 0.363	0.722 ± 0.363
He	0.796 ± 0.111	0.796 ± 0.217
F_{is}	0.034	0.182

Table 5. a) Within population measures of nuclear DNA genetic diversity calculated over 10 loci for 10 populations. N alleles, number of alleles; Ho, observed heterozygosity; He, expected heterozygosity and Wright's FIS with significance indicated at strict Bonferroni-corrected level (α=0.00050***). Population names as in Fig. 6.

	Group 1	Group 2	Group 3
N	181	113	16
Private alleles	7	14	1
Average±SD			
Nalleles	10.900 ± 4.977	12.700 ± 4.270	4.800 ± 1.398
Allelic richness	5.115 ± 2.731	7.372 ± 2.620	4.183 ± 1.179
Ho	0.588 ± 0.203	0.723 ± 0.228	0.524 ± 0.231
He	0.620 ± 0.203	0.771 ± 0.207	0.549 ± 0.182
F_{is}	0.051	0.062	0.047

Table 5. b) Within population measures of nuclear DNA genetic diversity calculated over 10 loci for k= 3. N alleles, number of alleles; Ho, observed heterozygosity; He, expected heterozygosity and Wright's F_{IS} with significance indicated at strict Bonferroni-corrected level (α=0.00050***). Population names as in Fig. 6.

Mitochondrial DNA sequences.

A total of 20 individuals from Spain, Portugal and Belgium was amplified and sequenced for the three different mtDNA regions (Control Region, ATP and ND5, Table 6) to examine if all the markers needed to be used to properly examine relative levels of genetic diversity and differentiation, or whether this could be achieved with fewer markers. For *mcr*, five haplotypes with nine variable sites were found (Table 7); for ATP, seven haplotypes could be differentiated with 11 variable sites and five haplotypes were identified for ND5 with eight variable sites. Median-joining networks were drawn for each marker (Fig. 10). There was no evidence that more information was obtained by using all three markers and therefore only the *mcr* was used.

Locus	Primer sequence	Fragment size (bp)	Ta (°C)
Control region [a]	ACCTCGGTCTTGTAAACC	623	46 and 53
	ACCAAATGAATGAAATCTCAG		
ATP [b]	CTAATATCAACACGACCTG	873	51
	TATCTCGTCATCACTGGTA		
ND5 [b]	GGTGCAACTCCAAATAA	1535	53
	GTTGCGAGTTTTTGGC		

Table 6. Characterisation of three primer pairs to amplify mitochondrial DNA regions in harbour porpoise. [a] derived from primers L15928 and HOOO34 (Rosel et al 1995, Kocher et al 1989); [b] Fontaine et al unpublished data.

mcr	Variable sites									Population		
	0	0	0	0	0	0	0	2	2			
	0	1	2	5	6	8	9	3	4			
	7	8	8	1	5	1	1	5	0	SP	PT	BEL
Hap_1	A	G	A	T	T	G	T	T	C	3	2	0
Hap_2	.	.	G	.	.	.	.	.	T	1	1	0
Hap_3	G	A	G	C	C	.	.	.	.	1	0	2
Hap_4	.	.	G	.	.	A	.	.	.	0	4	0
Hap_5	.	.	G	.	.	.	A	C	.	0	1	0

ATP	Variable sites											Population		
	0	0	0	0	0	0	0	0	0	0	1			
	0	2	3	3	4	5	6	7	8	9	0			
	3	6	5	6	4	9	1	6	0	2	3			
	8	2	6	3	5	5	3	3	9	9	6	SP	PT	BEL
Hap_1	C	G	C	T	G	T	C	A	A	C	C	1	0	0
Hap_2	.	.	.	.	.	.	.	.	G	.	.	4	5	0
Hap_3	T	A	T	C	.	C	T	.	G	.	.	1	0	0
Hap_4	.	.	T	.	.	.	.	.	G	.	.	1	1	0
Hap_5	.	.	T	.	A	.	.	.	G	.	.	0	1	0
Hap_6	.	.	.	.	.	.	.	.	G	G	G	0	1	0
Hap_7	T	A	T	C	.	C	T	T	G	.	.	0	0	2

ND5	Variable sites								Population		
	0	0	0	0	0	0	0	0			
	0	1	3	3	4	6	7	7			
	9	0	3	7	9	1	1	4			
	3	0	1	0	6	7	9	0	SP	PT	BEL
Hap_1	T	A	C	G	C	A	A	A	1	1	0
Hap_2	.	.	.	.	.	.	.	C	4	2	0
Hap_3	.	G	T	A	T	G	G	C	1	0	1
Hap_4	C	G	.	A	T	G	.	C	0	1	0
Hap_5	C	.	.	A	.	.	.	C	0	1	0

Table 7. Haplotypes and variable sites for the 3 genes (mcr 334pb, ATP 1061bp, ND5 1007bp) sequenced for samples from SP Spain, PT Portugal and BEL Belgium.

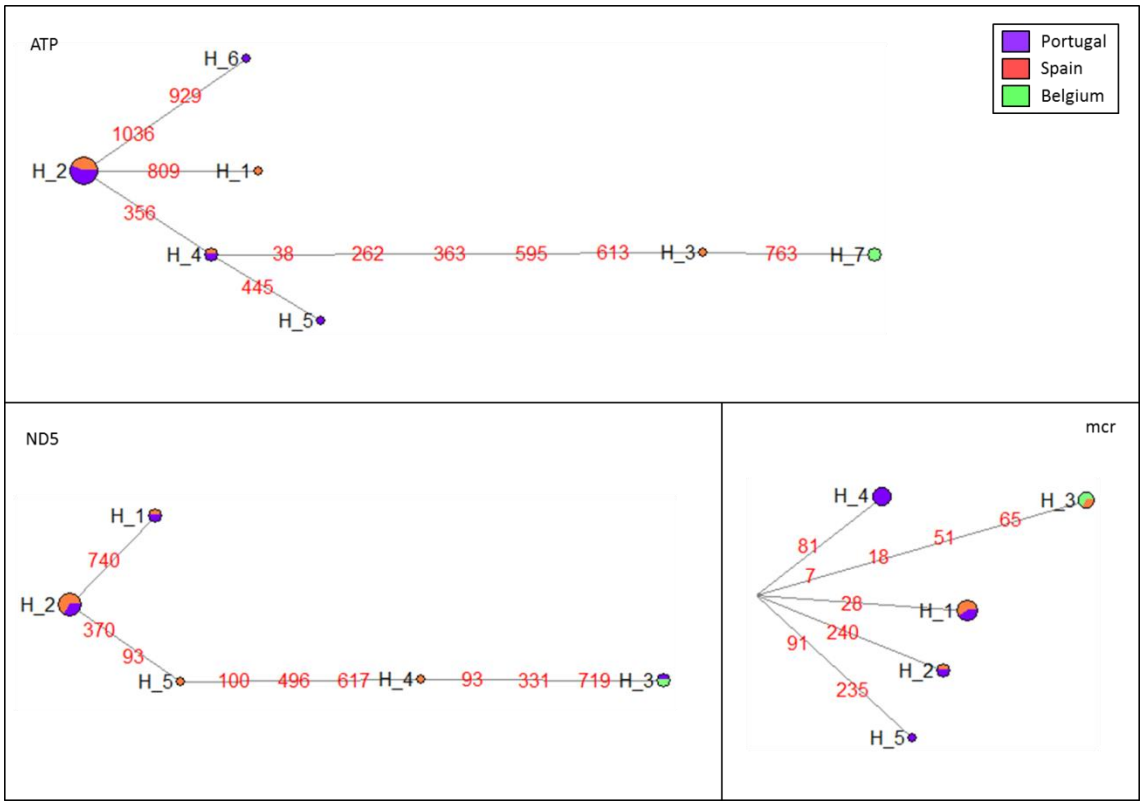


Figure 10. Haplotype network for ATP, ND5 and mcr occurring in Spain, Portugal and Belgium. Red numbers are the mutated positions.

A total of 167 samples from Spain, Portugal and Belgium were successfully sequenced for 488 bp of *mcr*. In order to allow direct comparison with sequences available in GenBank, the size of the sequences obtained in this study were truncated to 334 bp. This mtDNA dataset was combined with 1352 previously published mtDNA sequences all coming from harbour porpoises, in order to obtain a wide picture of the mtDNA structure (Fig. 11). One hundred and eleven different *mcr* haplotypes were found (Appendix II; correspondence between haplotypes and accession numbers of GeneBank is given in Appendix III); three haplotypes were newly discovered. Seventy-six polymorphic sites were found, with 69 transitions and 12 transversions. Occurrence of the haplotypes and relative frequencies for the nine populations and k=4 are shown in Appendix IV and Appendix V respectively. Unique haplotypes were found in all populations except Spain, and in all four groups of k=4. The most common haplotype (49.37% of the sequences) was Hap_4, which was present in SP, NE1, NE2, WGLD and ICL for populations, and was only absent in Group 4 for K=4.

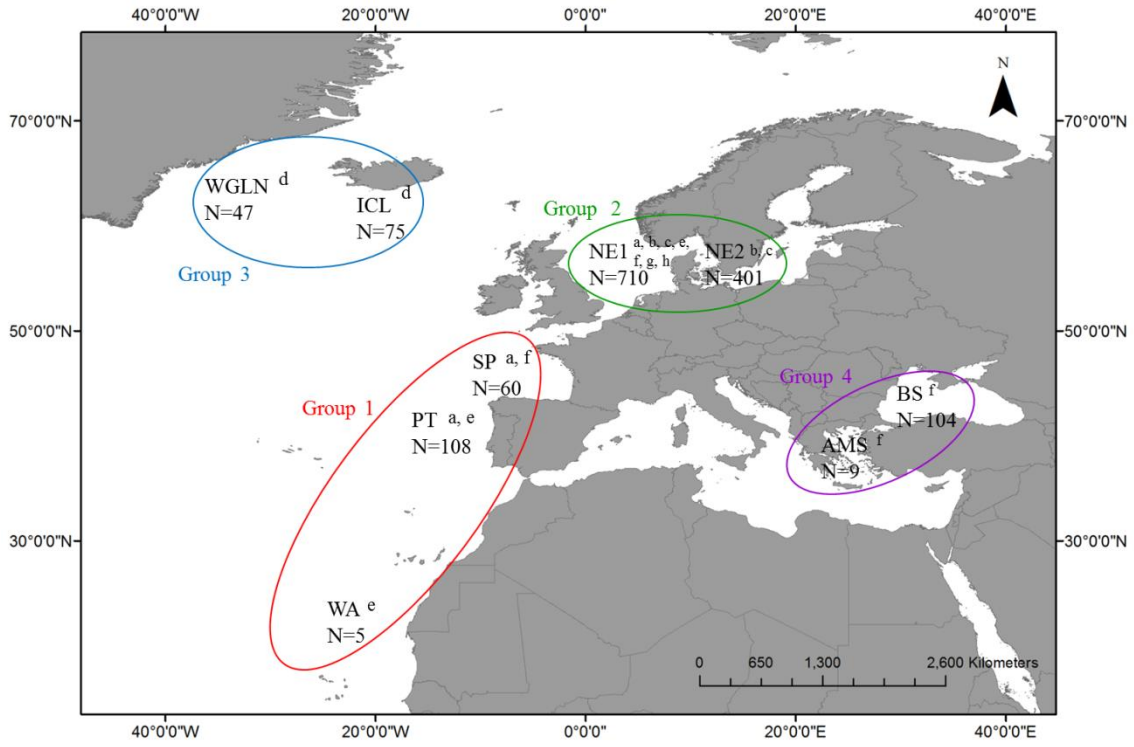


Figure 11. Sampling locations and sizes for harbour porpoise (*Phocoena phocoena*) for mtDNA analyses; WGLD West Greenland, ICL Iceland, NE1 North Sea, English Channel, Ireland/Celt area and Norway, NE2 Baltic area, SP Spain, PT Portugal, WA West Africa, BS Black Sea, Aegean and Marmara Sea AMS. [a], our study; [b], Tiedemann et al 1996; [c], Walton 1997; [d], Tolley et al 2001; [e], Tolley and Rosel 2006; [f], Viaud-Martínez et al 2007; [g], Wiemann et al 2010; [h], Alfonsi et al 2012.

The overall nucleotide diversity (π) and haplotype diversity (Hd) were estimated to be 0.0083 (± 0.0048) and 0.7320 (± 0.115) respectively (Table 8). Both estimates were smaller for NE2 and higher for ICL when looking for populations. For k=4 the smaller lowest estimates were for Group 4 and the highest for Group 3.

a)

Population	SP	PT	WA	NE1	NE2	WGLD	ICL
N	60	108	5	710	401	75	45
π (±SD)	0.0030 ± 0.0023	0.0030 ± 0.0023	0.0066 ± 0.0051	0.0064 ± 0.0039	0.0018 ± 0.0016	0.0110 ± 0.0063	0.0114 ± 0.0064
Hd (±SD)	0.5972 ± 0.0495	0.6284 ± 0.0321	0.8000 ± 0.1640	0.6675 ± 0.0179	0.3125 ± 0.0306	0.9491 ± 0.0130	0.9186 ± 0.0230
Tv/Ts	1/7	1/11	1/4	4/44	4/19	1/24	3/39

Population	AMS	BS
N	9	104
π (±SD)	0.0030 ± 0.0030	0.0026 ± 0.0021
Hd (±SD)	0.5000 ± 0.2652	0.4206 ± 0.0615
Tv/Ts	0/2	0/15

b)

Population	Group 1	Group 2	Group 3	Group 4
N	173	1111	122	113
π (±SD)	0.0033 ± 0.0024	0.0052 ± 0.0033	0.0112 ± 0.0063	0.0028 ± 0.0022
Hd (±SD)	0.6368 ± 0.0269	0.5586 ± 0.0176	0.9376 ± 0.0126	0.4488 ± 0.0604
Tv/Ts	1/11	7/52	4/44	0/16

Table 8. Within population measures of mitochondrial DNA genetic diversity: nucleotide diversity, π (±SD) and haplotype diversity, Hd (±SD), Tv/Ts; a) at K= 4, b) at the 9 populations studied. Population names as in Fig. 11.

Mismatch distribution analyses indicated that the SP, PT, WGLD and ICL populations had a genetic signal of a sudden expansion, exhibiting unimodal distributions with low raggedness indices (Fig. 12). Both the populations of North Europe and BS were in demographic equilibrium with high raggedness indices. However, only West Greenland had a significant p-value. Due to the small sample size of WA and AMS, results cannot be considered. For K=4, Groups 1 and 2 have low raggedness indices, fitting the expansion model, and 3 and 4 had high values, fitting the equilibrium, but only Group 4 has a significant p-value.

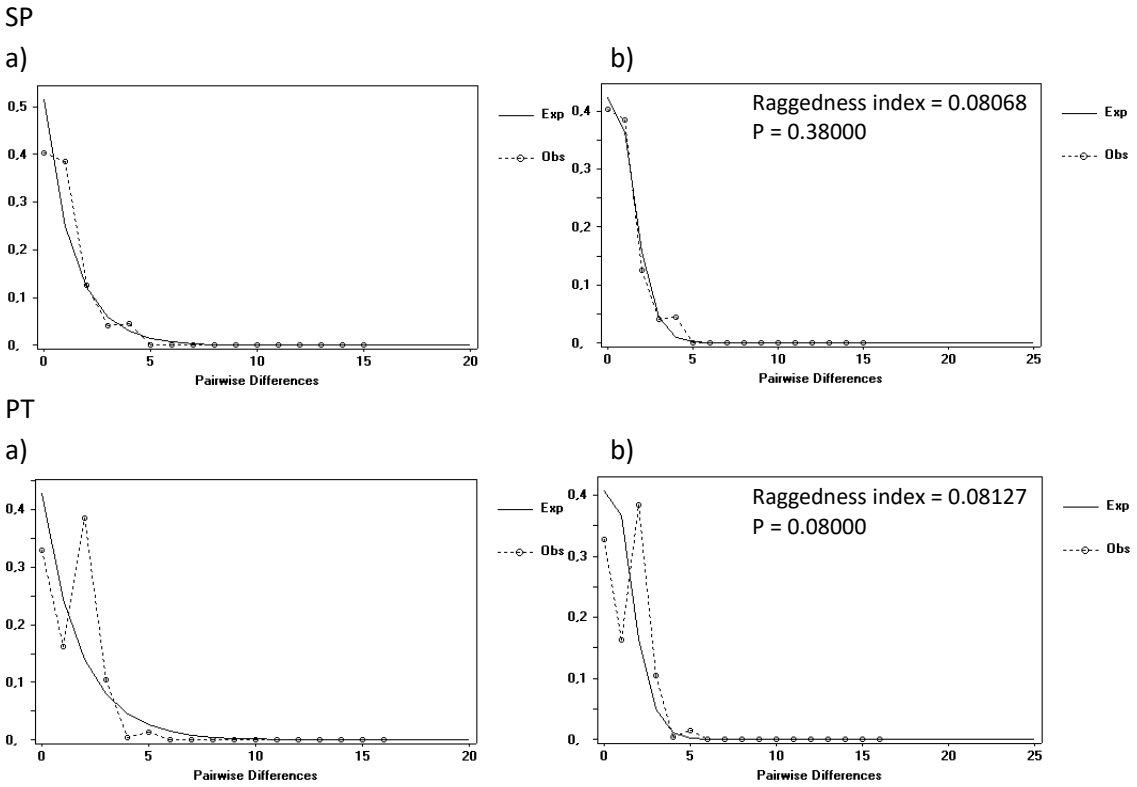
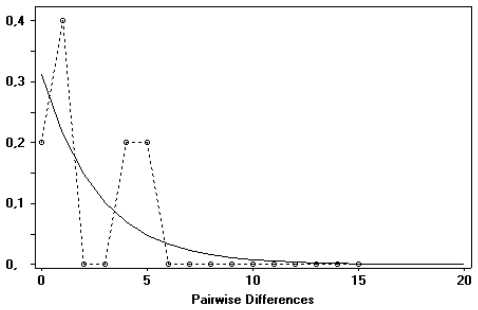


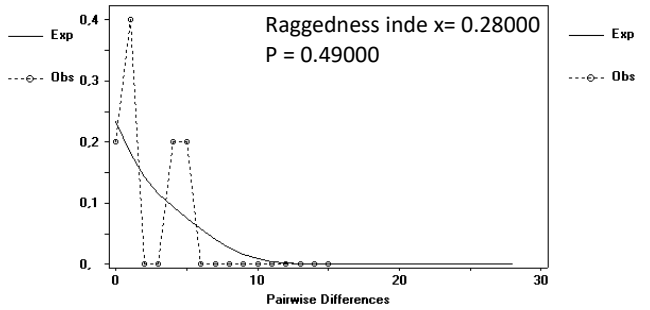
Figure 12. Mis-match distribution graphs calculated using the distance method Pairwise difference, for a) a constant population and b) a population growth-decline, for the 9 populations studied and K = 4 for the mitochondrial control region. Population names as in Fig. 11.

WA

a)

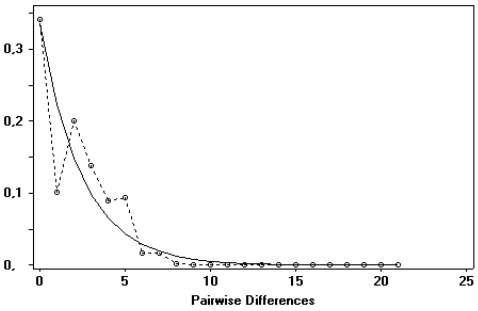


b)

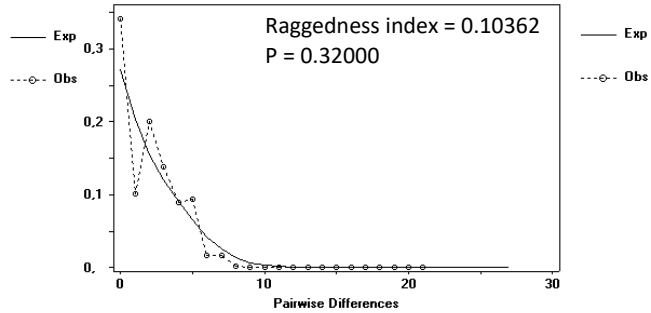


NE1

a)

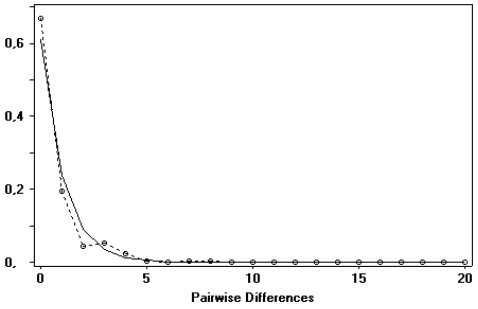


b)

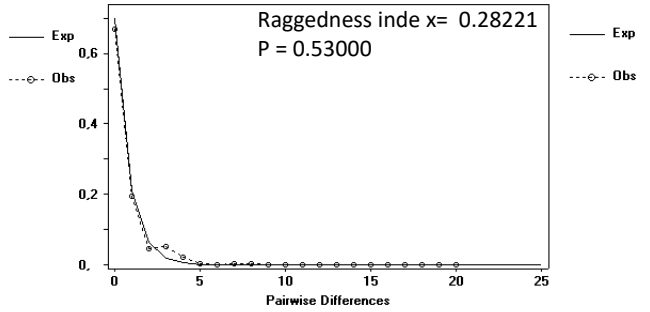


NE2

a)

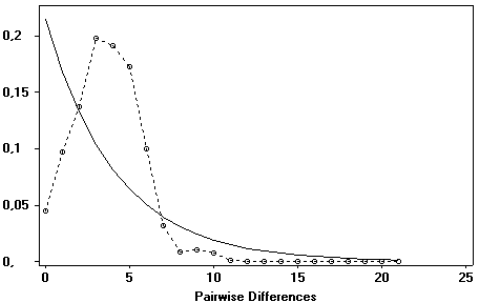


b)



WGLD

a)



b)

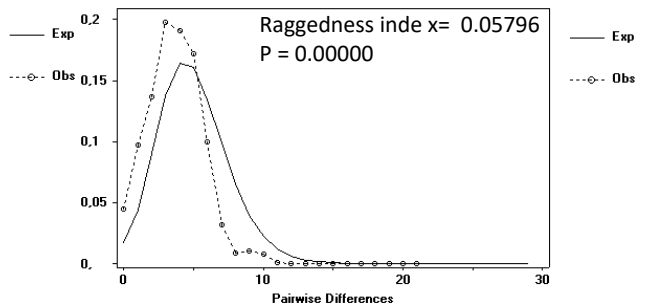
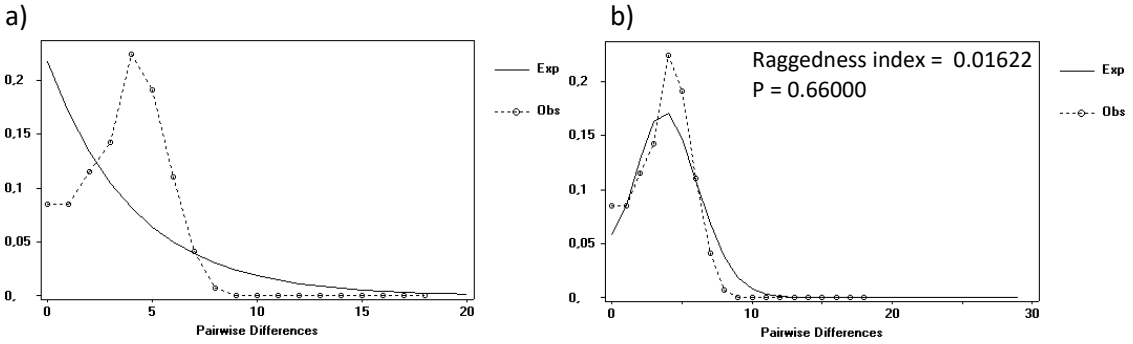
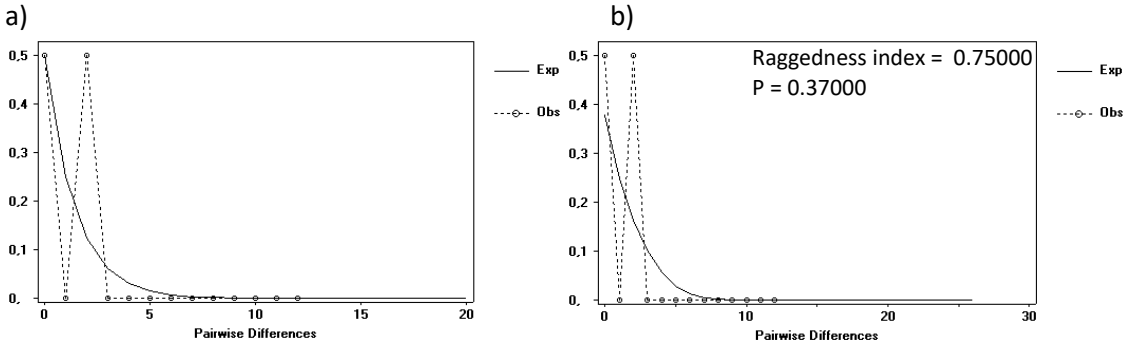


Figure 12. Continued.

ICL



AMS



BS

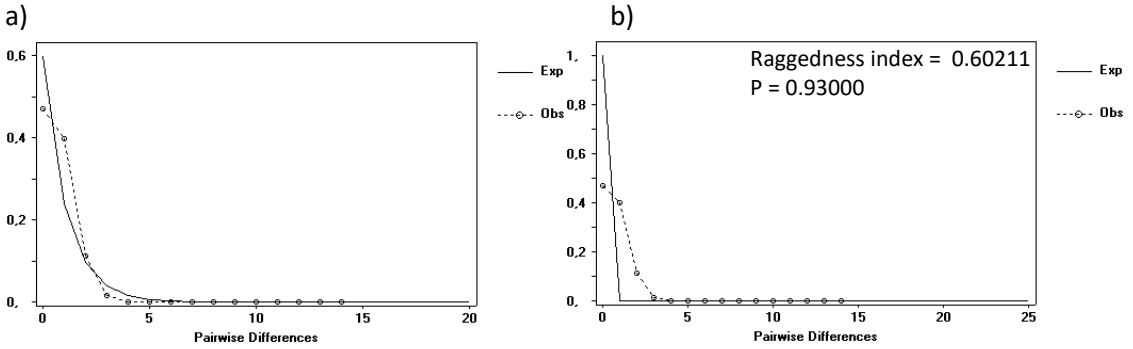
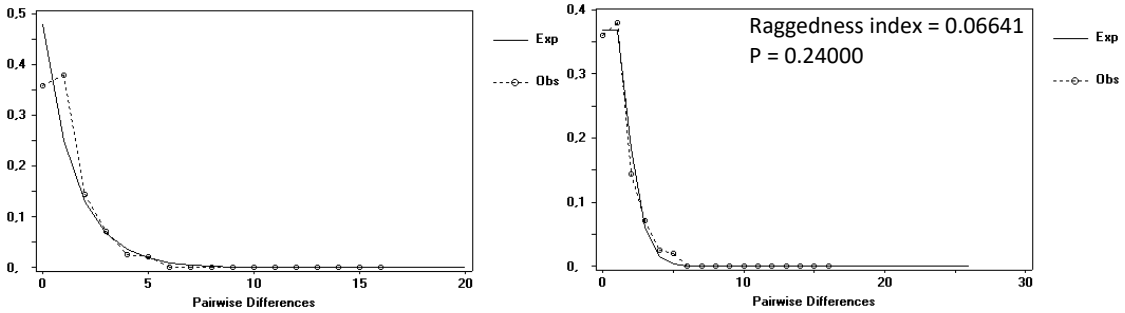


Figure 12. Continued.

.

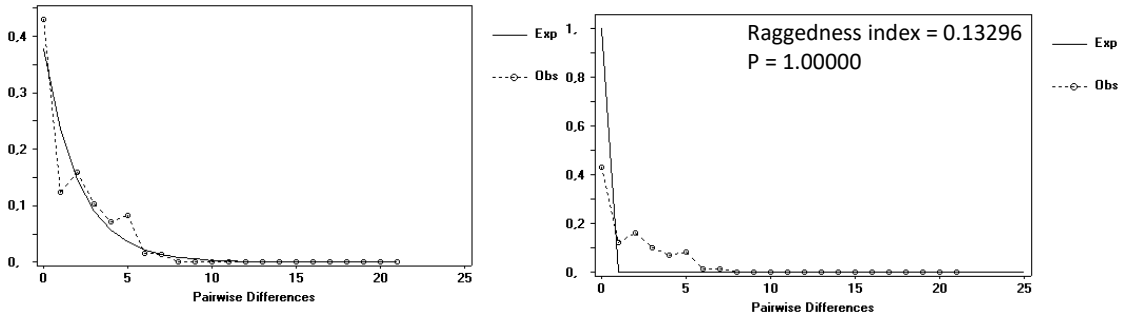
Group 1.

a) b)



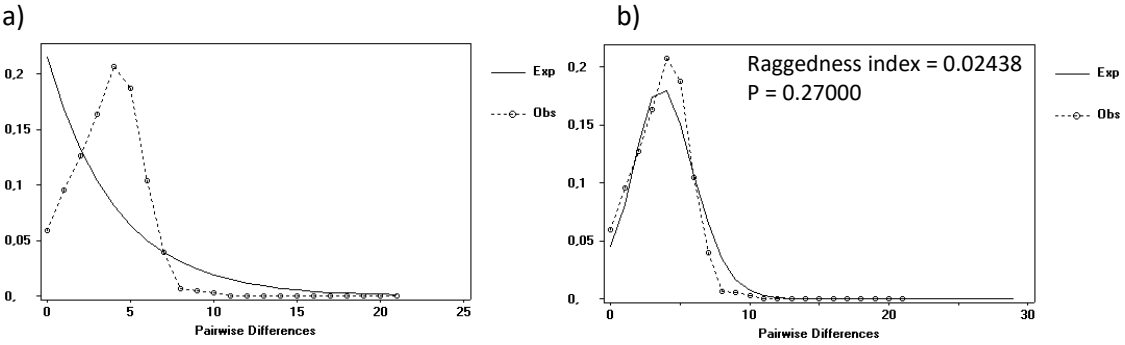
Group 2

a) b)



Group 3

a) b)



Group 4

a) b)

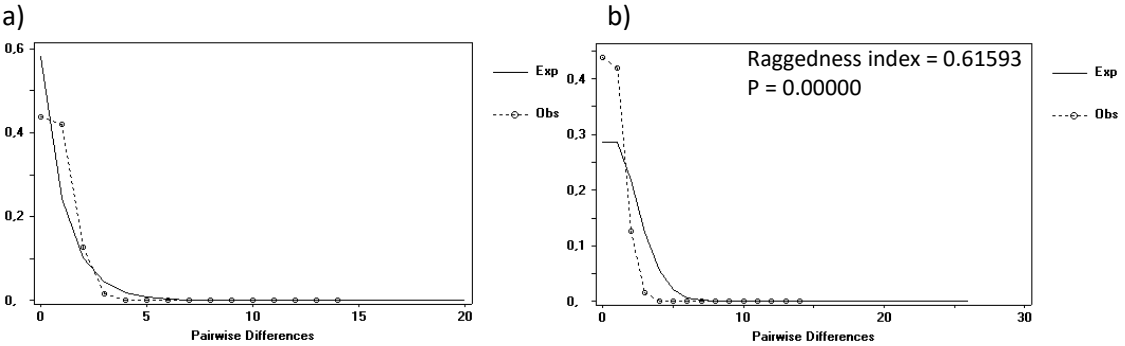


Figure 12. Continued.

A median-joining network was drawn for all the *mcr* haplotypes and coded according to a k=4 population subdivision (Fig. 13). The network showed five principal haplotypes (Hapl_4, Hapl_1, Hapl_62, Hapl_21, Hapl_44) with only one (Hapl_44) absent from the second group. Although there was no clear clustering based on population origin, haplotypes present in Group 4 formed a different group, sharing no haplotypes with the rest of the groups. As seen before, all groups had unique haplotypes.

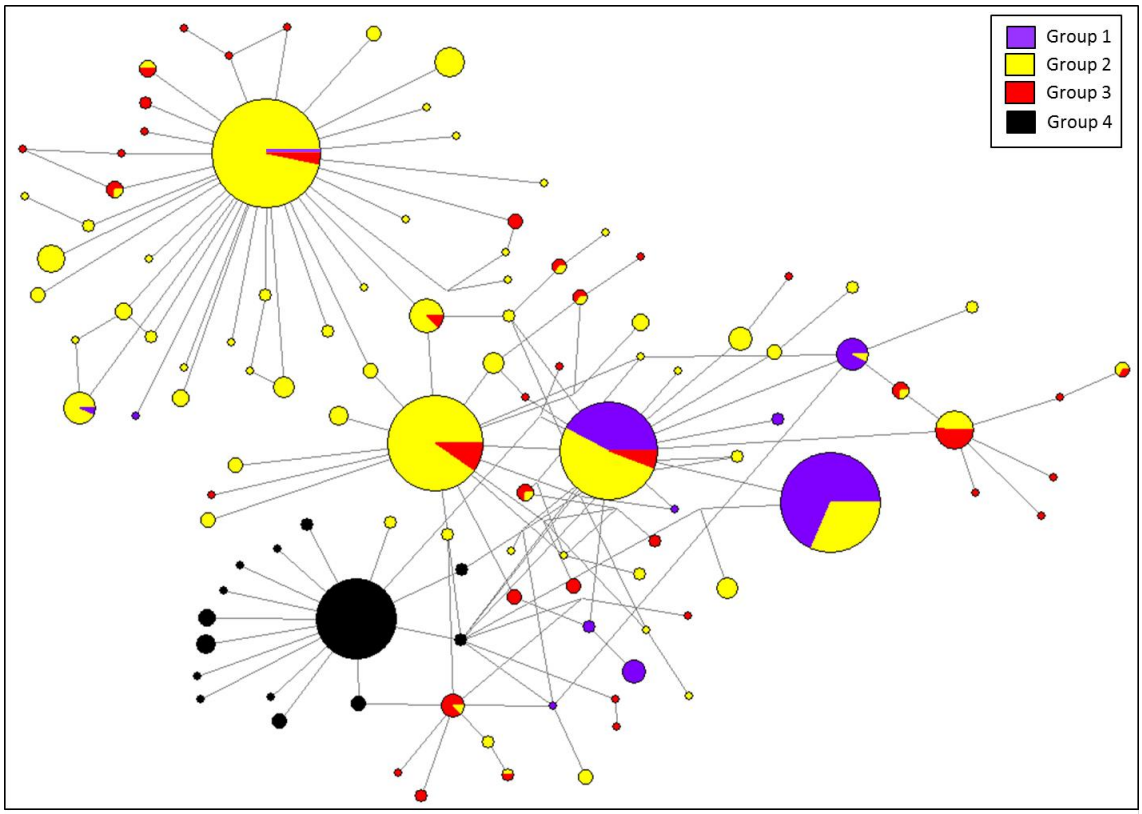


Figure 13. Haplotype network of haplotypes for mcr occurring in K = 4.

For Dxy, the biggest differentiation was found for AMS and BS versus the rest of populations from Europe (Table 13), WA and AMS being the most different populations (Dxy = 0.0204). The most similar populations were SP and PT (Dxy = 0.0030); other low values were found for NE1 versus NE2, and BS versus AMS. When populations were grouped using k = 4, Group 4 was the most different from the rest, in contrast Group 2 and 3 were the most similar.

There were significant genetic differentiations, expressed as F_{ST}, between all the populations except for SP versus PT and WGLD versus ICL (Table 13). The differentiation between AMS and BS was less significant than between the rest of locations. For k=4, all comparisons revealed significant differences.

a)

Population	N	SP	PT	WA	NE1	NE2	WGLD	ICL	AMS	BS
N		60	108	5	710	401	47	75	9	104
SP	60	-	0.0030	0.0084	0.0091	0.0114	0.0096	0.0104	0.0140	0.0125
PT	108	-0.00502	-	0.0088	0.0101	0.0125	0.0105	0.0113	0.0146	0.0131
WA	5	0.57066***	0.56226***	-	0.0129	0.0143	0.0118	0.0148	0.0204	0.0182
NE1	723	0.50955***	0.52648***	0.48962***	-	0.0048	0.0093	0.0088	0.0162	0.0139
NE2	418	0.86527***	0.86188***	0.86275***	0.16562***	-	0.0100	0.0086	0.0214	0.0192
WGLD	11	0.41688***	0.47007***	0.28688***	0.11406***	0.56318***	-	0.0112	0.0179	0.0184
ICL	84	0.43570***	0.48650***	0.32928***	0.06777***	0.43006***	0.01113	-	0.0184	0.0171
AMS	4	0.80998***	0.80992***	0.73705***	0.66285***	0.91529***	0.46061***	0.44661***	-	0.0040
BS	106	0.78091***	0.77612***	0.80736***	0.62905***	0.88802***	0.59041***	0.55274***	0.44716**	-

b)

Population	N	Group 1	Group 2	Group 3	Group 4
N		173	1111	122	113
Group 1	173	-	0.0101	0.0103	0.0127
Group 2	1116	0.62590***	-	0.0089	0.0149
Group 3	122	0.45173***	0.15864***	-	0.0170
Group 4	108	0.75833***	0.70157***	0.51335***	-

Table 9. Estimates of population differentiation for a) 9 populations, b) K= 4, expressed as Dxy (above diagonal) and FST (below diagonal) based on mitochondrial data. For F_{ST} **0,001 < P < 0.01 and ***P < 0.00001. N: sample sizes. Population names as in Fig. 11.

For *mcr*, AMOVA revealed significant divergence within groups among populations and within populations (Table 10). Most genetic variation occurred within populations (43.56%). The second largest variance component was attributed to divergence among groups (35.46%) but was not significant, while the smallest fraction of the variance was due to divergence among populations within groups (20.98%).

Regions	Degrees of freedom	Sum of squares	Variance components	P-value	Percentaje of variation
Among groups	3	554.999	0.67444	0.0948 ± 0.0085	35.46
Within groups among populations	5	304.246	0.39898	0.0000 ± 0.0000	20.98
Within populations	1510	1.250.862	0.82839	0.0000 ± 0.0000	43.56

Table 10. Analyses of molecular variance (AMOVA) for mitochondrial at the 9 populations.

The sex was known for 54 individuals from SP (28 females and 26 males) and 77 from PT (42 females and 35 males). To see if there was any difference between sexes a median-joining network was drawn (Fig. 14), showing that in Portugal males had more haplotypes than females and all haplotypes present in females were shared with males. Genetic diversity values expressed as nucleotide diversity and haplotype diversity from mitochondrial data were also calculated (Table 11). The nucleotide diversity was lower in Spanish samples than in Portuguese individuals. Spanish males had the lowest haplotype diversity of the four groups (k = 4).

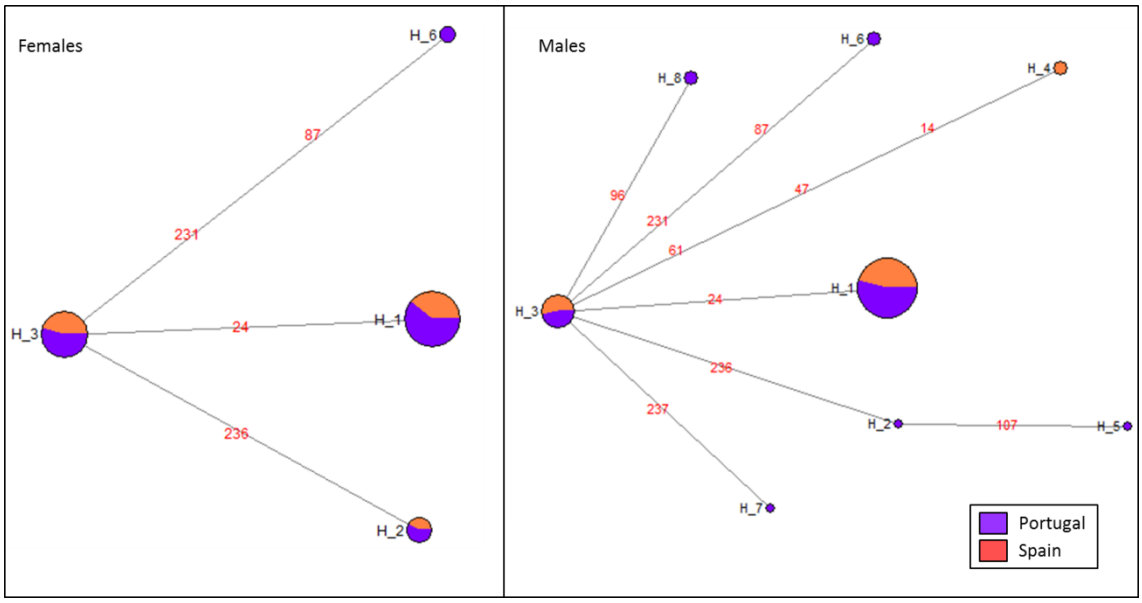


Figure 14. Haplotype network for 3 mcr for females and males from Iberian Peninsula.

Both Dxy and F_{ST} showed higher values for males than females when comparing these two populations (Dxy females = 0.0172, Dxy males = 0.0399, F_{ST} females = 0.0026, F_{ST} males = 0.0042).

Population	SP_F	SP_M	PT_F	PT_M
N	28	26	42	35
π (±SD)	0.0023	0.0027	0.0030	0.0042
Hd (±SD)	0.6123	0.4800	0.6307	0.6277

Table 11. Measures of mitochondrial DNA genetic diversity for females and males from Spain and Portugal: nucleotide diversity, π (±SD) and haplotype diversity, Hd (±SD). SP_F, Spain females, SP_M, Spain males, PT_F, Portugal females, PT_M, Portugal males.

Discussion

The salient feature of the present study is the high level of genetic structure that has been resolved using both microsatellite and mitochondrial DNA markers for harbour porpoises across the Northeast Atlantic and Black Sea. Some of these findings are consistent with previous studies, but other aspects provide new information to increase the understanding of the patterns, causes and consequences of genetic structure.

The Structure-based analyses of microsatellite structure identified three main groups: the Iberian Peninsula, the rest of Northeast Atlantic, and the Black Sea. This division is the same as previously found (e.g. Rosel et al 1995); however what was unexpected was that Structure separated Iberia from the other samples before it identified the Black Sea as a separate genetic grouping. Black Sea porpoises have previously been described as an isolated population and classified as the subspecies *Phocoena phocoena relicta* (Abel 1905), supported by genetic and morphological data (Rosel et al 1995, 2003, Gol'din 2004, Tolley and Rosel 2006, Viaud-Martinez et al 2007, Fontaine et al 2007, 2010, Galatius and Gol'din 2011, Tonay et al 2012).

In the Black Sea population several private alleles were resolved and overall this population had the smallest allelic richness. Fontaine et al (2012) detected a recent decline in the Black Sea population, which could explain the results of the present study, given the likelihood of increased effects of genetic drift leading to lower heterozygosity (Garner el at 2005). This population was found to be significantly different from the population of the Iberian Peninsula and moderately, yet significantly, different with the populations from France and England, but not significantly different from Belgium, Ireland and Scotland, which is surprising and could explain the results of the Structure-based analyses.

Also it was found that the mitochondrial haplotype diversity in the Black Sea and Aegean-Marmara Sea was the lowest of all populations studied. The same result was found in other studies (Rosel et al 1995, 1999 a, Tiedemann et al 1996, Tolley et al 1999, 2001, Tolley and Rosel 2006, Walton 1997, Wang and Berggen 1997, Wiemann et al 2010), though Wang and Werggen (1997) found even lower diversity in the Skagerrak and Kattegat.

A median joining network of mtDNA sequences highlights the isolation of the Aegean-Marmara Sea and Black Sea populations, which share only one haplotype with other populations. This difference is echoed by significant values for F_{ST} for mtDNA with the other

regions studied. A significant difference was also observed between the Aegean – Marmara Seas and the Black Sea, which is in accordance with the previous work of Viaud-Martinez (2007). Tonay et al (2012) supports the possibility of an isolated population in the Marmara Sea. Given that Fontaine et al (2012) did not detect significant differences between porpoises from the Aegean and Black Sea, this suggests that, despite now being isolated, Aegean Sea porpoises come from the Black Sea rather than the Atlantic population.

The mismatch distribution in the Black Sea showed a high raggedness index but no significant differences from the distribution expected under equilibrium, which does not agree with the idea of demographic expansion once the Black Sea was reconnected with the Mediterranean previously reported (Fontaine et al 2012).

The other main separation resolved with the Structure analysis was the Iberian Peninsula and the rest of Northeast Atlantic. Here, no private alleles were found in Portugal and the Basque Country, though this may be due to small sample size. Heterozygosity for the Iberian Peninsula, was higher than values found by Fontaine et al (2007).

Using the microsatellite markers, we detected genetic differentiation between Galicia and Portugal and the rest of the populations. Similar results were obtained in previous studies (Tolley and Rosel 2006, Fontaine et al 2007, 2010, Alfonsi et al 2012), suggesting the isolation of the Iberian population that has been estimated to occur approximately 300 years ago (Fontaine et al 2010) during the “Little Ice Age”. In contrast, among the other populations of Northeast Atlantic, differences were not significant.

Spain and Portugal had similar mitochondrial nucleotide diversity, though haplotype diversity was lower in Spain. Both mitochondrial DNA diversity measures were lower than in all the other populations except those in the eastern Mediterranean

The most frequent haplotype found in the Iberian population (Hap_1) was also the most frequent in France (Alfonsi et al 2012). West Africa and South Portugal share one haplotype (Hap_6), which was not found in previous studies (Tolley and Rosel 2006). These results may show the connection between those areas and reveal, especially for the population in West Africa, the need to increase the number of samples to increase our knowledge of the relationship between areas.

In the mismatch analyses, the raggedness index for Portugal was high and showed a multimodal distribution, but it was not significantly different from expectations for a population that has been growing. The same was true for Spain.

A primary objective of this study was to provide more resolution on population structure among Iberian harbour porpoise populations. It was found that there was no significant pattern of population genetic structure in harbour porpoises along the Iberian Peninsula coast. This result is different to those found for other species present in the Atlantic Iberian peninsula, such as the bottlenose dolphin (Fernández et al 2011) which shows a strong genetic differentiation between southern Galician dolphins and animals from neighbouring locations that have been recently defined as another management unit (Fernández et al 2011, ICES 2014).

Despite female philopatry having been detected for this species in previous population genetic studies for certain areas (Wang et al 1996, Tiedemann et al 1996, Andersen et al 1997, 2001, Walton 1997, Rosel et al 1999 b, Tolley et al 1999, Wiemann et al 2010), no significant differences were found between patterns of genetic structure derived from males and females across Spain and Portugal. That said there were some differences in nucleotide and haplotype diversity, with Portuguese individuals being more diverse than Spanish.

There are several processes that may explain the genetic differences of porpoises from the Iberian Peninsula and North West Africa from more northerly populations. Levels of divergence clearly cannot be explained by isolation by distance but instead are likely to be associated with population separation based upon oceanographic differences in relation to sea surface temperature, chlorophyll concentration, salinity, water turbidity, ocean currents, depth, slope or upwelling areas (Hoelzel et al 1998, Fullard et al 2000, Natoli et al 2005, Möller et al 2007, 2011, Bilgmann et al 2007, Stockin et al 2013, Richards et al 2013, Gaspari et al 2013). This correlation between genetic distance and environmental differences was defined as “Isolation by Environmental Distance” (IBED, Mendez et al 2010) and was previously described for the franciscana (*Pontoporia blainvillen*, Mendez et al 2010), the humpback dolphin (*Sousa chinensis*, Mendez et al 2011) and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*, Ansmann et al 2012).

The existence of upwelling conditions in West Iberia and North West Africa increases the productivity of the area, hence presumably enhancing prey abundance thus providing suitable conditions for porpoises (e.g. Fraga 1981, Figueiras et al 2002, Fontaine et al 2007, 2014,

Alfonsi et al 2012, Chapters 3 and 4). In the north of the range of the Iberian population, in the Bay of Biscay, strong barriers to gene flow were detected between this population and populations of the rest of North Europe, that coincide with profound differences in environmental characteristics. The warmer and deeper waters in the Bay of Biscay make this area unfavourable for porpoises. The southern boundary may be due to historical isolation with the Black Sea as the Mediterranean Sea became warmer and oligotrophic after the Last Glacial Maximum (Tolley and Rosel 2006, Fontaine et al 2010).

Oceanographic features themselves are not likely to affect the distribution of the cetaceans directly, but the most important factors in determining their occurrence and movements are thought to be the prey abundance and distribution (Hastie et al 2004), that have thermal and saline sensitivity (Fullard et al 2000, Jøgersen et al 2005). For harbour porpoise, the small size of which limits the amount of stored energy so that it can survive for only short periods without feeding (Kastelein et al 1997), a relatively continuous availability of the prey is important (MacLeod et al 2007). Therefore, the presence of a cold water species, such as harbour porpoise, in the Iberian Peninsula can be explained by the existence of the upwelling along the Iberian coast, with cold and highly productive waters (Fiùza 1983, Fraga 1981, Ambar and Fiùza 1994, Figueiras et al 2002), that increases the presence of porpoise prey and allows them to persist south of the Bay of Biscay (OSPAR 2000) and which can influence their genetic structuring.

The last group of populations differentiated using Structure was the one of North Europe (France, Belgium, Ireland, England and Scotland), which were not significantly different for microsatellite loci, and had similar levels of allelic richness, with the highest allelic richness found in Ireland. This is consistent with Fontaine et al (2007) and Alfonsi et al (2012). Heterozygosity values for Scotland and England were higher than those found previously (Andersen et al 2001, Fontaine et al 2007).

Estimates of genetic diversity for the mitochondrial control region showed an east-west trend with highest values found for West Greenland and Iceland which is in accordance with previous studies (Rosel et al 1999 a,b, Tolley et al 2001).

West Greenland and Iceland populations were shown to be significantly different to the populations of the Northeast Atlantic and there were no significant differences between them.

In the present study all populations analysed were significantly less diverse than those in the Western North Atlantic, supporting previous comparisons of these areas (Tiedemann et al 1996, Wang et al 1996, Rosel et al 1999 a, b, Tolley et al 2001), and Atlantic porpoises are also less diverse than the Pacific ones (Rosel et al 1995).

The Northeast Atlantic and Iceland showed the mismatch distributions expected under expansion. However, West Greenland is better described as a population that has been stationary for a long time.

Overall the genetic data suggest that the Iberian Peninsula and West Africa must be considered as one unique population. It is a distinct genetic grouping that would be consistent with the assertion (Fontaine et al 2014) that they should be described as a separate subspecies, *Phocoena phocoena meridionalis.* The recognition of this isolated population is essential to assess threats that can affect them, such as by-catch in commercial fisheries (Jefferson and Curry 1994, Read 1994, Donovan and Bjorge 1995, Berggren et al 2002, Stenson 2003, Read 2013). Furthermore, it is the basis for the creation of specific management plans and the definition of SACs as required by the EU Habitats Directive.

Given the extent of genetic structure driven by ongoing ecological processes, it would be interesting to examine whether there are equivalent differences in ecological tracers (e.g. stable isotopes and fatty acid profiles, levels of contaminants) which could reveal how genetic divergence equates to ecological separation. It would also be interesting to provide a genome-wide pattern of genetic divergence across populations to examine the extent to which ecological divergence drives adaptive genetic differentiation as well as neutral divergence.

CHAPTER III

Modelling harbour porpoise habitat preferences along the Galician coast from boat survey data

Ángela LLavona, Jose A. Martínez-Cedeira, Pablo Covelo, Alfredo López, Vasilis Valavanis, José V. Vingada and Graham J. Pierce.

Conceived and designed surveys and sampling: ALL, JAM-C, PC, AL, GJP.

Collected the data: ALL, JAM-C, PC, AL.

Designed the analysis: GJP and ALL

Analyzed the data: ALL.

Contributed materials/analysis tools: AL, VV, GJP.

Wrote the paper: ALL.

Edited the text: GJP.

Provided constructive comments on the manuscript and approved the final document: GJP, AL, JVV.

Abstract

Distribution, abundance and population dynamics of cetaceans are considered as indicators of Good Environmental State of the EU's marine waters under the Marine Strategy Framework Directive. Spain, like several other Member States, has proposed indicators based on small cetacean abundance, distribution and bycatch, for several species including porpoises. Thus the understanding of porpoise distribution is a key requirement.

In this study cetacean habitat modelling was used as it represents a potentially powerful tool for predicting cetacean distributions and understanding the ecological processes determining these distributions. Targeted boat surveys were carried out in Galician coastal waters during the years 2003 - 2010. Results showed that the detection of porpoises was influenced by sea state, the detection of porpoises decreasing with values of Douglas greater than 2. The best boat speed for monitoring harbour porpoises is around 6 knots and the probability of detecting harbour porpoises increases with field-of-view width. There was also interannual variation with a significant increase in the number of sightings in 2005 and no detections in 2006. In contrast, no significant differences in porpoise presence were seen between months or in relation to depth. Several environmental variables were found to be important to explain the presence of porpoises. Porpoises were mostly seen in waters with medium temperatures. As chlorophyll concentration and the depth of the eutrophic zone increase there was an increase in porpoise presence. Finally there were positive relationships between number of sightings and both seabed slope and its facing to the South.

Results show that porpoises are likely related to areas with conditions of high productivity, which will ultimately affect the higher trophic levels through food chain-related processes, and may be good for the development and aggregation of the most important prey of harbour porpoises in Galicia such as blue whiting, *Trisopterus* spp, silvery pout (*Gadiculus argenteus*) and *Trachurus* sp. Then porpoise distribution is likely to reflect foraging opportunities. This is important as, by remaining close to food resources, porpoises are able to meet the energetic demands of maintenance, growth and reproduction.

Knowledge of the environmental conditions and areas in which porpoises were seen with higher probability can help define suitable areas for their conservation. While the association with high productivity may help to define preferred areas, in a mobile species it is also essential to take into account variation in distribution, not only seasonally but from year to year.

Introduction

Spain is one of the countries of the Europe with highest marine biodiversity (IUCN[1], Convention on Biological Diversity[2]); it has more than 8000 km of coastline, along which around 58% of the human population is located. Galicia is the region of Spain with the second longest coastline (1195 km) with 78% of the population located at the coast (Aguas de Galicia. Xunta de Galicia[3]). It is the main fishing region of Spain and one of the most important in the world, with 87 fishing ports and more than 4843 fishing boats (Spanish Ministry of Agriculture and Environment 2013); most of them are small boats working in inshore waters using traps, trawls, gillnets and longlines to target molluscs and crustaceans. Around 2000 boats work in offshore (littoral) waters; longlines, trawls and gillnets are used to take species such as hake (*Merluccius merluccius*), blue whiting (*Micromesistius poutassou*), scad (*Trachurus trachurus*) and monkfish (*Lophius piscatorius, L. budegassa*), while purse seiners target sardine (*Sardina pilchardus*), scad and anchovy (*Engraulis encrasicholus*).

Galician waters also have an important community of cetaceans with 22 species (Covelo et al 2009), including the harbour porpoise. The population of this species in the Iberian Peninsula has been described as genetically isolated from the rest of the North East Atlantic (Fontaine et al 2007, 2014, see also Chapter II). This species is known to be present all year round (López et al 2002, López 2003, Pierce et al 2010). Hammond et al (2013) estimated the abundance of this species in shelf waters from SW France, along the Atlantic coast of Spain and Portugal to the Strait of Gibraltar to be 974 (CV 0.84) individuals. Abundance in Galicia and Cantabria has been estimated as 683 porpoises (CV 0.63; López et al 2013), and the Galician population had been previously estimated to be of 386 (CV 0.71) individuals (López et al 2012).

Porpoises are mainly piscivorous, and in Galician waters they feed mainly on blue whiting (*Micromesistius poutassou*) and *Trachurus* spp (Pierce et al 2010, Santos unpublished data). Santos et al (2014) estimated a food daily consumption per individual of 1.96 kg, representing 4.44% of the body weight of an average porpoise at Galicia, implying that the resident population could take 509 tonnes of fish annually.

The harbour porpoise is designated as ”vulnerable” in Spain (Catálogo Nacional de Especies Amenazadas, Law 4/1989, 2000) and is included in Annex-II of the Habitats Directive, thus requiring the designation of Special Areas of Conservation (SACs) by EU Member States in

[1] http://iucn.org/about/union/secretariat/offices/europe/resources/country_focus/spain/
[2] https://www.cbd.int/countries/profile/default.shtml?country=es#facts
[3] http://augasdegalicia.xunta.es/es/4.1.htm

whose waters the species occurs. The study of its populations is a priority issue and IWC (International Whaling Commission) and ICES (International Council for the Exploration of the Sea) recommended studies to determine the population structure of this species and develop an appropriate management plan (IWC 1998) in order to reduce negative impacts on their populations. See Chapter I and II, and Fontaine et al (2007, 2010, 2014) for further discussion of stock structure for this species in European seas.

Anthropogenic threats on the health of the marine environment and its natural resources grow year by year (European Commission 2014), including underwater noise, pollution, shipping, offshore development and fishery bycatch.

Incidental by-catch in commercial fisheries is considered as the main threat for cetaceans worldwide, including harbour porpoise (Jefferson and Curry 1994, Read 1994, Donovan and Bjorge 1995, Berggren et al 2002, Stenson 2003, Siebert et al 2006). Due to the high fishing activity in Galicia a high number of by-catches is likely in the area. By-catch rates in Galician waters have been estimated from stranding data (López et al 2003, López et al 2012, Read et al 2012), observer trips on fishing vessels (López et al 2003), and interviews with fishermen (López et al 2003, Goetz et al 2014), and all these sources of information, except the observer trips, suggest that the overall cetacean by-catch rate is unsustainably high. Common dolphins are apparently frequently caught in gillnets in Galicia (López et al 2003), and data from strandings showed that 23% of the dolphins were fishery by-catches (López et al 2002). It was confirmed or diagnosed as the cause of death in between 14% (bottlenose dolphin) and 29% (Risso's dolphin) of the strandings of the most frequent species recorded (López et al 2002). Slightly over 40% of porpoise strandings in Galicia have indications of by-catch (Read et al 2012), although, together with pilot whale and striped dolphin, harbour porpoise represented only 5.1% of the total cetacean bycatch reported during interviews with fishers (Goetz et al 2014). It has been estimated that the incidental by-catch of porpoises in Galicia (around 49 animals annually) exceeds the 1.7% of the population annually (López et al 2012, Read et al 2012), a limit considered as an unacceptable interaction by ASCOBANS (1997).

The high incidence of by-catch, in addition to other potential anthropogenic threats such as pollution, overfishing and disturbance suggest that there is a need to develop conservation management plans for Iberian harbour porpoise, and indeed this has already been recognised by the Galician government. Several biological issues should ideally be addressed prior to conservation management plan design, particularly when focusing on a possibly endangered

species or population. In fact, it is necessary to define species distribution, abundance, genetic status and threats (Stenson 2003).

Two EU Directives are especially relevant to porpoise conservation. The Habitats Directive requires the creation of SACs for harbour porpoises, as mentioned above. The general aim of SACs is the maintenance or restoration, to a favourable conservation status, of the natural habitats and/or the populations of the species for which the site is designated. In addition the Habitats Directive prohibits deterioration or destruction of breeding sites or resting places (Article 12), and requires avoidance of their disturbance (Article 6) particularly during the period of breeding and migration (Article 12) for all species listed in Appendices II and IV of the Directive. At present, Spain has not designated any SACs for porpoises. In order to identify suitable sites, we need to understand distribution, movements and habitat use by porpoises, in particular to identify "hot spots" that are regularly used by the species and/or are important for foraging, rearing calves, etc.

Under the Marine Strategy Framework Directive (MSFD), as is also the case for many other marine taxa, aspects of the distribution, abundance and population dynamics of cetaceans are considered as indicators of Good Environmental State (GES) of the EU's marine waters. Spain, like several other Member States, has proposed indicators based on small cetacean abundance, distribution and bycatch, for several species including porpoises (VV.AA. 2014). In addition, the MSFD requires coordination of monitoring at regional seas level and the above-mentioned indicators have all been proposed as Common Indicators for the OSPAR region. Thus the understanding of porpoise distribution is a key requirement to allow assessment of environmental status and to determine if the effort carried out to achieve GES by 2020 through management measures, as required by the Marine Directive, has been successful or not.

Cetacean–habitat modelling represents a potentially powerful tool for predicting cetacean distributions and understanding the ecological processes determining these distributions. It has already been used to incorporate this variability into management applications, including improvement of abundance estimates, development of marine protected areas, and understanding cetacean–fisheries interactions (Redfern et al 2006). Cetacean data used in habitat modelling may come from both dedicated and opportunistic studies including ship, aerial, and acoustic surveys, as well as individual tagging studies (Redfern et al 2006).

Since 1990 the NGO CEMMA (Coordinadora para o Estudo dos Mamíferos MAriños) has studied marine mammals and sea turtles in Galicia and, since 2003, targeted boat surveys have been carried out in Galician coastal waters. Data recorded during these surveys, during the years 2003 - 2010, are used for this study to describe and model i) spatial and ii) temporal trends in harbour porpoise distribution in the study area, and iii) compare its distribution with those of the other resident species present in Galician coastal waters, such as the bottlenose dolphin); iv) quantify the factors that affect the observers' capacity to detect porpoises during boat surveys; and v) study the environmental characteristics of the habitat that determine the presence of harbour porpoises at the study area and compare it with previous studies of the habitat use by cetaceans of that area (Fernández 2010, Pierce et al 2010, Spyrakos et al 2011, Méndez-Fernandez et al 2013; Fernández et al 2013).

The present study will provide essential data on the harbour porpoise to improve knowledge of distribution and ecology of the species in Galician waters, to permit the development of an adequate management plan, and to provide baseline data for the comparison of its situation with future work on the species that will help us to determine whether GES has been reached by 2020 at Galician waters as required by EU regulations.

Materials and methods

Study area.

The study area is the Galician coast in the northwest Iberian Peninsula (Fig. 15). The coastline (1195 Km) features cliffs, sandy beaches, and a series of "rías", which are flooded tectonic valleys of moderate depth. The continental shelf of Galicia is narrow (20 - 35 km wide) and the coast is influenced by northerly winds during spring and summer, which produce a seasonal upwelling near the coast that influences the entire shelf area (Fraga 1981), and a southward surface current. This oceanographic feature makes the northwest Iberian Peninsula an area of high biodiversity with an elevated number of cetacean species and it is one of the most important fishing areas of the world (Covelo et al 2009, Spanish Ministry of Agriculture and Environment, 2013).

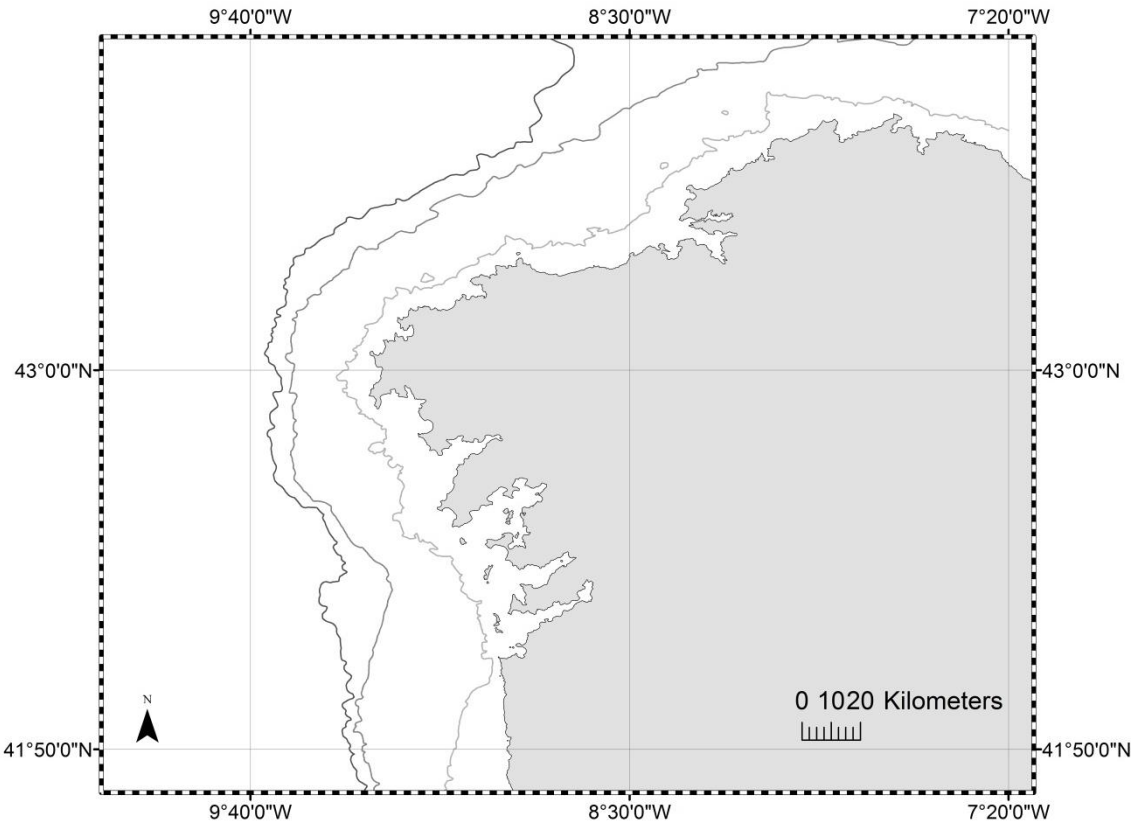


Figure 15. Study area.

Survey design and data collection.

From 2003 to 2010 systematic cetacean surveys were carried out along Galician coast from March to October. The number and distribution of surveys varied between years because of their dependence on different projects. Also, several vessels were used but most of the surveys were conducted using the *Nauja*, a motor-sailing vessel of 21 m length (n=84 surveys). The other vessels used were the *Íbero*, a 16 m motor-sailing vessel (n=24), the 16 m motor-sailing vessel *Black Knight* (n=1), the 32 m motor-sailing vessel *Nieves* (n=4), the 33 m long-liner *Santiago Apóstolo* (n=5), the 30 m long-liner *Anxuela* (n=2) and the 5.25 m motorboat *Elda dos* (n=1).

A survey was considered as the part of each trip during which observations took place. Transects did not follow a systematic design but they aimed to cover the area as evenly as possible within constraints due to weather conditions and location of ports. In particular, because the distribution of cetaceans is known to be related with depth (e.g. Hooker et al 1999, Carretta et al 2001, Cañadas et al 2003, Santora 2012), surveys aimed to cover the full range of depths over the continental shelf and slope. Although exact depth was used in the modelling, depth was also classified as "inside rías", "less than 100 m" (outside the rías), "100 – 200 m" and "more than 200 m" to use in some other analyses. Transects were designed to cross the isobaths perpendicularly and to go as far as possible from the coastline depending on the number of hours available for sampling in each survey. Because the two main ports were located inside the Rías of Arousa or Vigo, the area from the port to the limit of the ría was surveyed more often. Average travel speed was around 6.4 knots (CV 0.23).

In 2008 an additional project to monitor cetaceans in Galician coastal waters ("A favor del Mar: la ruta del Íbero 2008" funded by Fundación La Caixa) was carried out, so there was more effort in shallower waters than during the other years of study.

A minimum of 3 observers searched for cetaceans using binoculars or by naked eye, at different heights depending on the boat (from 2 m to 8 m above sea level): one of the observers was on the starboard side, searching a sector from 350° to 90°, another one on the port side, searching a sector from 270° to 10°, and in the case of the *Santiago Apóstolo* and the *Anxuela* a third observer was at the bow searching a sector from 270° to 90°. Depending on the number of observers present during each survey, the number of teams varied. At least one person per team was an observer with experience in cetacean observation.

Each survey was divided into 1 hour periods. If the number of observers was sufficient to establish several teams, each one worked 1 hour and rested until the next working period. If there were not enough observers, observation periods could last several hours, with rest breaks so that observation was not continuous and the duration of the observation periods varied depending on the survey.

Another person recorded, each 20 min, general data such as hour, vessel location, speed, direction and number and identity of observers working, and environmental data such as depth, Beaufort and wind direction, Douglas, swell height, visibility and (estimated) visible track width. Additional data were recorded if one of these variables changed significantly within the period of 20 min interval. The tracks were recorded in real time on a computer using the program OziExplorer (http://www.oziexplorer.com/).

A sighting consisted of the detection of one or more cetaceans. When there was doubt about the identification of the species or even the sighting itself, the observers checked it with binoculars. For each sighting, data were recorded as follows: time, boat position, angle from the bow, distance from the boat to the animals, species, group size estimates, environmental data, and behaviour of the cetaceans (swimming (direction of travelling), resting, feeding, jumping, interactions with conspecifics (described), interactions with other species or boats). Two types of sightings were differentiated: 1) systematic, when cetaceans were detected by the observers during observation time, 2) opportunistic, when animals were detected by persons who were not in the working team. The surveys also carried out photo-ID work on bottlenose dolphins. When this species was observed and weather conditions were suitable, the observation effort was suspended while photographs were taken.

All this information was recorded on standardized forms, and then transferred to computer. All the locations recorded by hand were mapped to detect and correct possible errors.

Environmental data.

A number of potential explanatory variables were considered for the analysis of habitat use. These were: latitude, longitude, sea surface temperature (SST), chlorophyll concentration (CHL), depth of the euphotic zone (ZEU), photosynthetically active radiation (PAR), depth (DEP), seabed slope (DEP_SL), seabed aspect (DEP-AS), and their standard deviations (SST-STD, CHL-STD, ZEU-STD, PAR-STD, DEP-STD, DEP_SL-STD, DEP-AS-STD).

The study area is well monitored in terms of monthly satellite imagery. MODISA (Moderate Resolution Imaging Spectroradiometer Aqua at 4 km spatial resolution Level-3 datasets) sea surface temperature distribution (SST in ^{o}C), sea surface chlorophyll concentration (CHL in mg/m^3), photosynthetically active radiation (PAR in Einstein/m^2/day), and euphotic depth (ZEU in meters) were downloaded through Oceancolor Web, NASA's online Distributed Active Archive Center. These monthly satellite datasets were downloaded in HDF (Hierarchical Data Format) and converted to ArcGIS grids through specific routines developed in AML (Arc Macro Language) for the workstation version of ArcGIS (ArcInfo). Bathymetry (DEP in meters at 800 m spatial resolution) was downloaded from GEBCO_08 (General Bathymetric Chart of the Oceans) and bathymetry slope (DEP_SLO) and aspect (ASP) were calculated in radians by applying the corresponding Z factor for the average latitude of the study area.

Mean environmental and bathymetry parameters were calculated for each sampling point using a buffer zone of 20 km around each point. The procedure was carried out in the workstation version of ArcGIS using the grid zonal function 'zonalstats' for calculating mean and standard deviation (zonalstats function with the {moment} argument).

Statistical analysis.

To analyse the significance of the variation of the sighting rates between depths classes and years, and with group size, χ^2 tests were carried out.

Before the modelling, data exploration followed the Zuur et al (2010) eight-step protocol (1- detection of outliers in response (Y) and explanatory (X) variables; 2- study the homogeneity of y; 3- study the normality of y; 4- investigate “zero trouble” (i.e zero inflation) in Y; 5- study the collinearity of different X; 6- study the relationship between Y and X; 7- search for interactions; and 8- study the independence of Y (i.e., autocorrelation)).

To follow these steps, boxplots, conditional boxplot and Cleveland dotplot / Dotcharts were created and correlations and Variance Inflation Factors (VIF) were calculated. When the response variables were binomial, no histograms or QQ plots were plotted. The result was that some variables needed to be removed (bearing, SST-STD, CHL-STD, DEP-STD and DEP_SL-STD) although none needed to be transformed (except in the case of wind direction, which is a circular variable and was split into north-south and east-west components).

Three response variables were defined: harbour porpoise presence, number of groups and presence of calves. Finally only the first one was studied because most of the sightings were only of one group of porpoises and there were very few sightings with calves.

The model selection was carried out in three-steps:

1- model the covariates affecting the observer;

2– model the spatiotemporal trends in sightings;

3– model the environmental effects that may affect the presence absence of harbour porpoises. For the first step the covariates studied were: boat speed, Beaufort and wind direction, Douglas sea state scale, visibility, swell height, visible width (Width_Field) and boat identity (the latter accounting for differences in platform height, etc). The wind direction was transformed to degrees, then to radians and finally to sine and cosine (Sin(WRad), Cos(WRad)), to have the northing and easting components. In this case when there was no wind Sin(WRad) and Cos(WRad) were considered as not available (NA). The final best model was then used as a "base model" for the next steps. In the second one the variables included were year, month, latitude and longitude (degrees). Finally, in the third step instead of year, month and location, the covariates studied were the environmental data: SST, SST-STD, CHL, CHL-STD, ZEU, ZEU-STD, PAR, PAR-STD, DEP, DEP-STD, DEP_SL, DEP_SL-STD, DEP-AS, DEP-AS-STD. The last of these (i.e. DEP-AS and DE-AS-STD) were also transformed to sin and cosine (DEP-AS-sin, DEP-AS-cos).

Generalised additive models (GAMs) were used to relate presence of harbour porpoises and explanatory variables as they permit non-normal distributions of response variables, and non-linear relationships between continuous covariates and the response variable, which are described with non-linear smooth functions (Hastie and Tibshirani 1990). As such they are suitable to capture non-linear cetacean-habitat relationships (Redfern et al 2006). GAMs can be used if the response variable is binary, discrete or continuous. In this case, the response variable harbour porpoises sighting was presence/absence data, the distribution selected was binomial and a logit link function was used. Covariates were used as smoothers with k = 3 for covariates affecting the observers (because variables like visibility are measured on a short ordinal scale), k= 4 for environmental covariates and k = 5 for year as the relationship was not expected to be very simple and there are 8 years of data; only the boat identity variable was nominal. The purpose of limiting k is two-fold. Firstly, for variables with few unique values (e.g. Beaufort) it permits a smooth curve to be fitted. For environmental variables it is a means of avoiding overfitting, or fitting unrealistically complex relationships (Zuur et al 2007).

For the model selection, firstly all covariates were studied one by one. The best single explanatory variable model was selected and new models were investigated by adding each remaining covariate one by one to obtain the best model with two explanatory variables. This process continued until the best model was found. If, at some of the steps, there were several good models, the process was followed independently from each of these candidate models. The main criterion for the model selection followed was the Akaike's Information Criterion (AIC) which measure the goodness of fit and the number of parameters in the model (Zuur et al 2007), and the deviance explained by the explanatory variables of the model. In addition, where the AIC was uninformative about whether it was necessary to add an additional variable (e.g. AIC values differed by less than 2), F tests were used to compare nested models. If several models were found to be final best models, they were all selected.

For the validation of the final model, plots of the residuals versus fitted values to confirm homogeneity of variance, were used.

All these analyses were carried out using the software R.2.11.1 and Brodgar 2.7.2 (Highland Statistics Ltd).

Results

Boat survey effort and sightings.

A total of 111 boat surveys was carried out from 2003 to 2010 and from March to October in Galician waters (Fig. 16), corresponding to 843.7 h and 9680.4 km of effort, and a total of 359 cetacean sightings was recorded (Table 12).

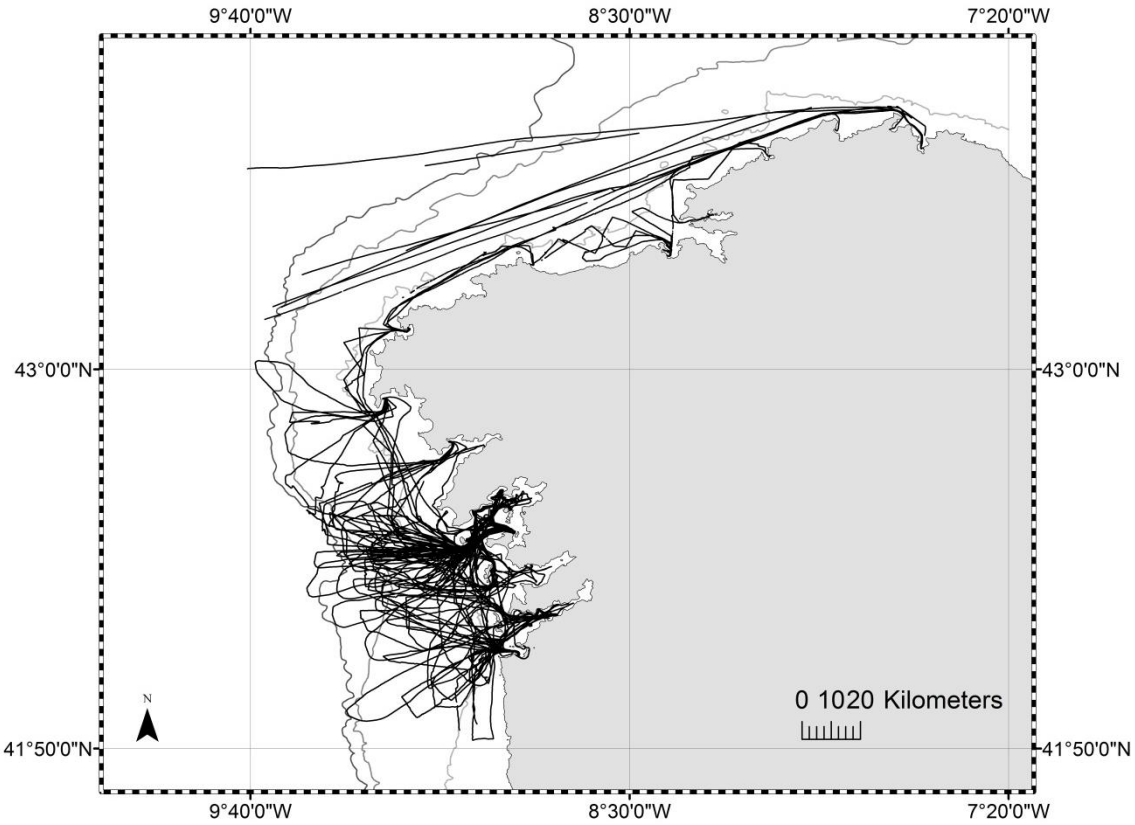


Figure 16. Boat surveys along the Galician coast from 2003 to 2010.

Due to economic issues and the dependence of different projects, the number and distribution of surveys varied between years. The km and km^2 covered, nº of sightings (total and of harbour porpoises), hours of sightings (total and of harbour porpoises), and total and per year encounter rates are shown in Table 12.

The year with most surveys (N=23) was 2008 (when an additional project was running, see methods), and the year with fewest was 2010 (N=8). Survey effort (Table 12) was highest in 2007 and 2008, and was lowest in 2010.

Year	Nº Surveys	Effort Km	Km^2	Effort h	Nº Total sightings	PPH sightings	Sightings h	Sightings PPH h	ERh	ERh PPH	ERkm	ERkm PPH
2003	13	982.2	1384.7	98.4	35	1	11.19	0.03	0.36	0.01	0.04	0.001
2004	12	1097.0	1630.0	95.3	56	6	16.26	0.67	0.59	0.06	0.05	0.005
2005	17	1583.1	2370.8	151.4	67	13	27.00	1.17	0.44	0.09	0.04	0.008
2006	9	1003.6	1001.9	78.9	33	0	3.55	0	0.42	-	0.03	-
2007	17	1621.4	2387.7	132.0	51	4	9.07	0.12	0.37	0.03	0.03	0.002
2008	23	1594.9	1967.1	140.9	68	4	14.50	0.22	0.48	0.03	0.04	0.003
2009	12	1040.2	1640.3	85.0	26	1	4.48	0.05	0.31	0.01	0.02	0.001
2010	8	758	1360.5	56.8	23	2	5.60	0.13	0.41	0.04	0.03	0.003
TOTAL	**111**	**9680.4**	**13743.0**	**843.7**	**359**	**30**	**91.66**	**2.38**	**0.43**	**0.04**	**0.04**	**0.003**

Table 12. Number of surveys, total km of effort, Km^2 covered, total hours of effort, total hours of sighting, total hours of sightings of harbour porpoises, total number of sightings, number of harbour porpoise sightings, and encounter rates (per hour ERh, and kilometres ERkm) calculated per year and in total.

Two home ports (O Grove and Vigo) were used for most of the surveys, and areas closer to these ports were better surveyed, especially in years with more surveys. The distribution of effort by depth class was also different each year. The proportion of survey time spent "inside rías" was highest in 2003 (around 50%; Fig. 17 a); 2006 was the year with the highest proportion of time spent at "more than 200 m", while in 2008 the survey extended along the whole Galician coast and the proportion of time spent at "less than 100 m" was higher than in the other years.

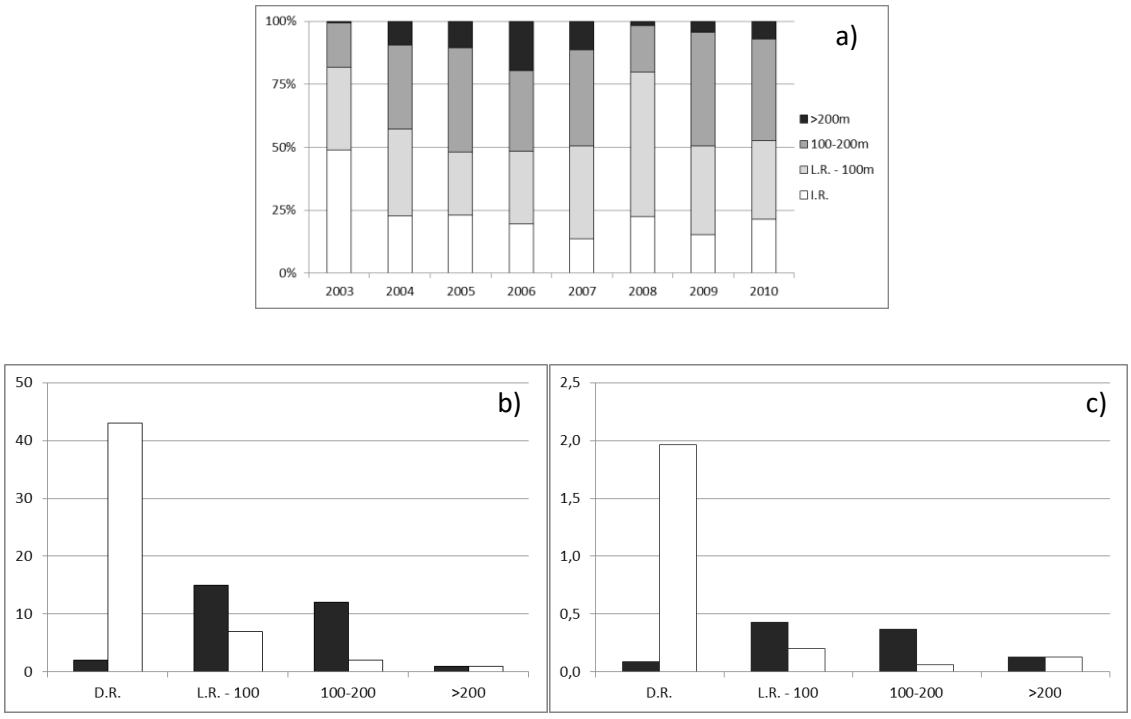


Figure 17. Distribution of the depth classes a) for the survey effort per year, b) for sightings of harbour porpoises (black) and bottlenose dolphins (white), and c) for sightings of harbour porpoises and bottlenose dolphins corrected by effort (km) multiplied by 100. L.R. limit of Rías, I.R. Inside Rías.

For all cetacean species, the years with most sightings were 2005 and 2008 (67 and 68 sightings respectively), while in 2010 only 23 sightings were recorded. The encounter rate (per hour and km surveyed) was highest in 2008 and lowest in 2007.

The most commonly recorded species of cetacean were common dolphin (*Delphinus delphis*) (53.3% of sightings), bottlenose dolphin (*Tursiops truncatus*) (16.1%) and harbour porpoise (*Phocoena phocoena*) (8.6%). Other species observed were long-finned pilot whales (*Globicephala melas*), Risso's dolphin (*Grampus griseus*), striped dolphin (*Stenella*

coeruleoalba), minke whale (*Balaenoptera acutorostrata*) and fin whale (*Balaenoptera physalus*) (Table 13a). The order of importance of the species does not change when expressed as sightings per hour of effort (Table 13 b).

a)

SPECIES	2003	2004	2005	2006	2007	2008	2009	2010	TOTAL	% TOTAL
Delphinus delphis	18	32	39	13	23	43	11	16	195	54.32
Tursiops truncatus	12	6	4	6	10	12	4	1	55	15.32
Phocoena phocoena	1	6	13	0	4	4	1	2	31	8.63
Globicephala melas	0	1	5	1	3	0	1	0	11	3.06
Grampus griseus	0	2	0	2	1	1	3	0	9	2.51
Balaenoptera acutorostrata	0	0	1	1	2	1	3	1	9	2.51
Balaenoptera physalus	0	0	0	3	1	0	0	0	4	1.11
Stenella coeruleoalba	0	0	0	1	0	0	0	0	1	0.28
Unidentified odontocetes	4	8	4	4	4	7	3	3	37	10.31
Unidentified mysticetes	0	1	1	2	3	0	0	0	7	1.95
TOTAL	**35**	**56**	**67**	**33**	**51**	**68**	**26**	**23**	**359**	**100**

b)

SPECIES	2003	2004	2005	2006	2007	2008	2009	2010	Average
Delphinus delphis	0.183	0.126	0.258	0.165	0.061	0.305	0.129	0.282	0.228
Tursiops truncatus	0.122	0.024	0.026	0.076	0.027	0.085	0.047	0.018	0.064
Phocoena phocoena	0.010	0.024	0.086	0	0.011	0.028	0.012	0.035	0.033
Globicephala melas	0	0.004	0.033	0.013	0.008	0	0.012	0	0.011
Grampus griseus	0	0.008	0	0.025	0.003	0.01	0.035	0	0.012
Balaenoptera acutorostrata	0	0	0.007	0.013	0.005	0.01	0.035	0.018	0.012
Balaenoptera physalus	0	0	0	0.038	0.003	0	0	0	0.006
Stenella coeruleoalba	0	0	0	0.013	0	0	0	0	0.002
Unidentified odontocetes	0.041	0.031	0.026	0.051	0.011	0.050	0.035	0.053	0.046
Unidentified mysticetes	0	0.004	0.007	0.025	0.008	0	0	0	0.008
TOTAL	0.356	0.220	0.442	0.418	0.136	0.483	0.306	0.405	0.421

Table 13. Number of sightings per year and species, a) in total and b) per hours of effort.

The years in which the highest number of species (7) was seen were 2006 and 2007, while in 2003 only 3 species were identified. Common dolphin and bottlenose dolphins were seen in all years; striped dolphin was seen only in 2006.

Both the highest number of cetacean sightings and the highest encounter rate were recorded in 2008. Fewest sightings were seen in 2010 although the lowest sightings rate was in 2007.

Breaking down observations into 20 minute periods, only fin whale was never seen during the same period as other species, and porpoises were only once detected with unidentified odontocetes during the same period. In the only sighting of striped dolphins, common dolphins and unidentified odontocetes were also seen.

For this study we are going to focus on harbour porpoise sightings.

A total of 30 sightings of harbour porpoises was recorded, with a total sightings duration of 2.38 hours (Table 12). They were seen at less than 100 m depth (outside the Rías) and between 100 - 200 m (Fig. 17 b and 18 a). The year with most porpoise sightings was 2005, while no porpoises were registered at 2006. Porpoise encounter rate (per hour) was the third highest after the common and bottlenose dolphin (Table 13 b). Encounter rate for porpoises was highest in 2005.

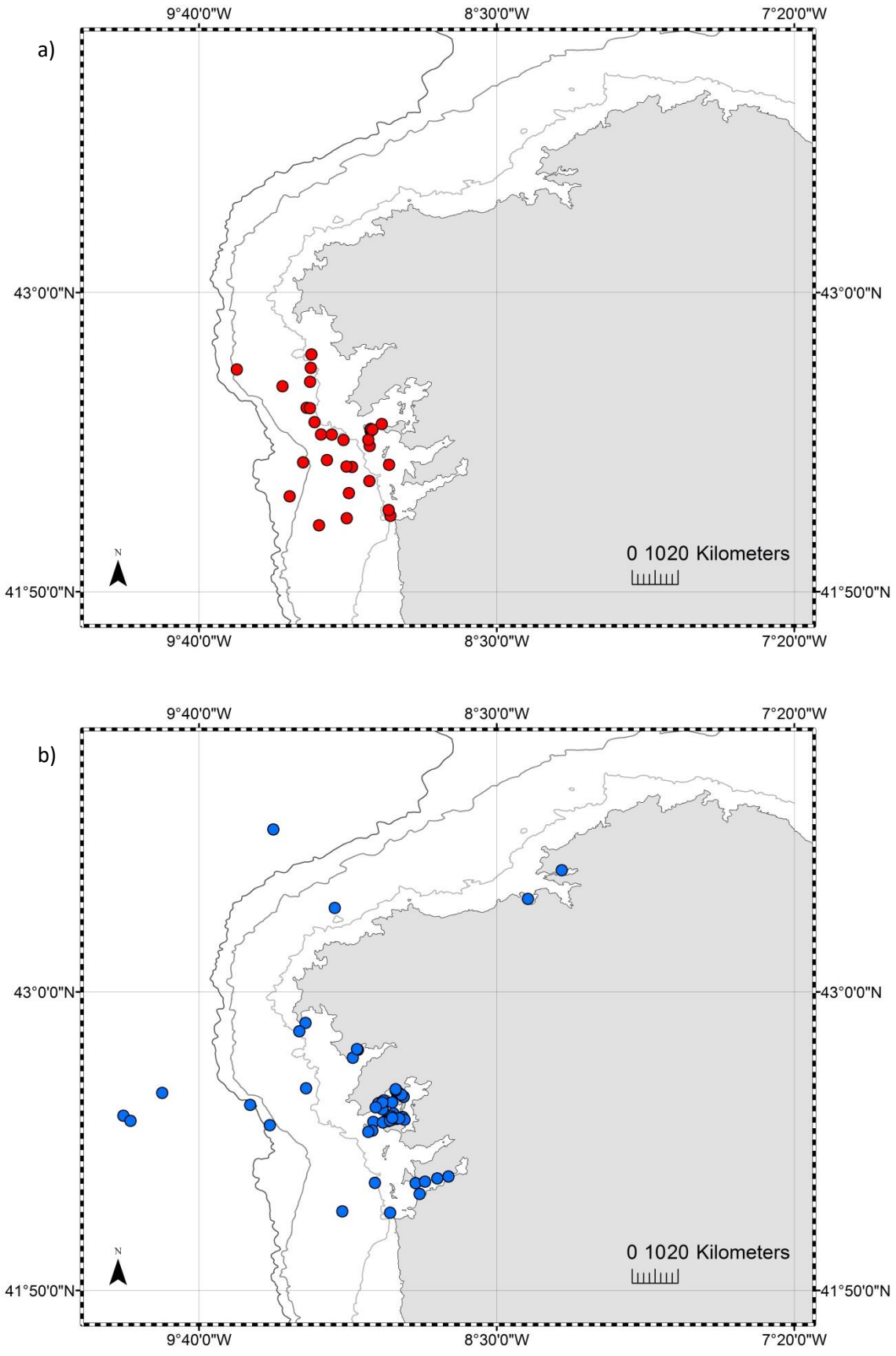


Figure 18. Representation of the sightings recorded on boat surveys from 2003 to 2010 for a) harbour porpoise sightings and b) bottlenose dolphin sightings.

Porpoise sightings per year do not follow the same pattern as sightings of all species (Table 12, Fig. 19 a): while 2008 was the year with most cetacean sightings and 2010 the year with least, porpoises were seen more often in 2005 and none were seen in 2006. Over the course of the year most porpoise sightings were recorded in June, July, September (the month with the maximum number of sightings) and October (Fig. 19 b). If the number of sightings is corrected by the number of hours of effort per year (Fig. 19 c), general tendencies are the same, but the peak in porpoise sightings in 2005 is smaller. In the case of the seasonal pattern, once effort is taken into account, the peak in September disappears, as this month had more effort than the rest, and peaks are now seen in June and October (Fig. 19 d).

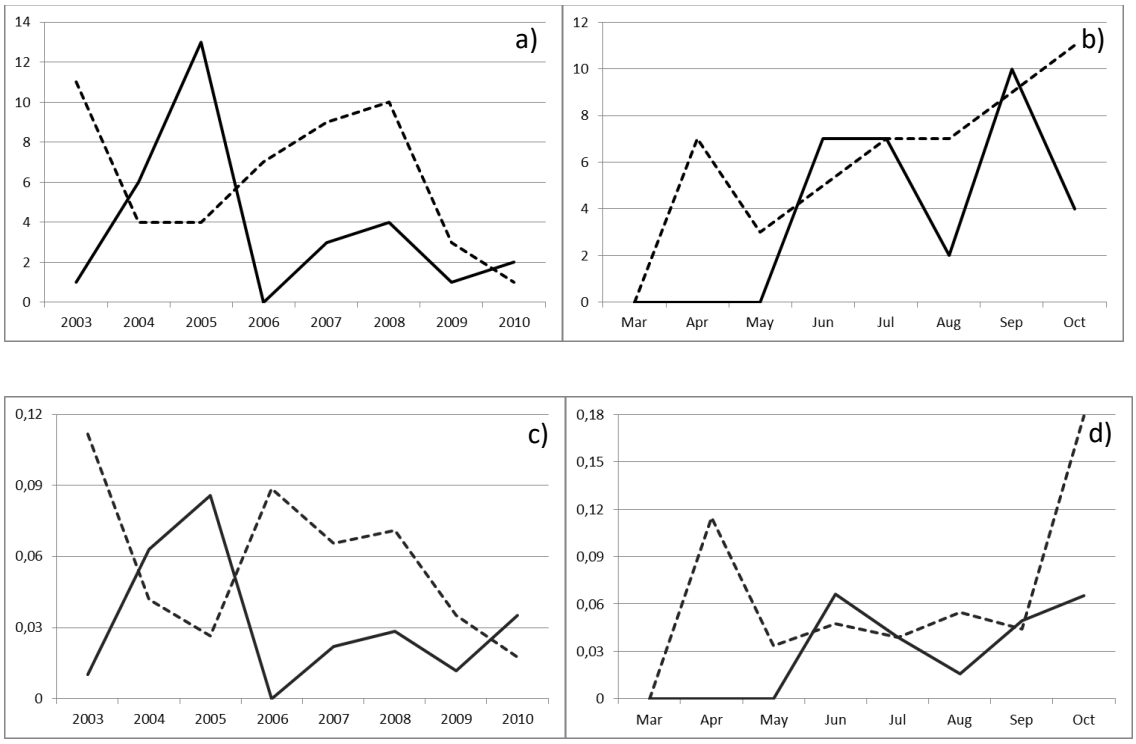


Figure 19. Number of sightings of harbour porpoise (black line) and bottlenose dolphin (dash line) per a) year, b) month, c) year and d) month corrected by effort (h).

The number of porpoises per group each year was similar across the eight years of study (Fig. 20 a) ranging from 1 to 4 individuals. To study the significance of the variation of the group size between years, it was necessary to define 3 groups of size classes: 1 or 2 individuals, 3 individuals, and 4 to 6 individuals; it was also necessary to group the years two by two. The variation was not found to be significant ($\chi 2 = 7.56$, d.f. 5). The number of groups of harbour porpoises with calves was very low and they were seen only in 2004 and 2008 (Fig. 20 b). As the number of sighting with calves was very low it could not be used as a response variable and therefore no modelling for calves was carried out.

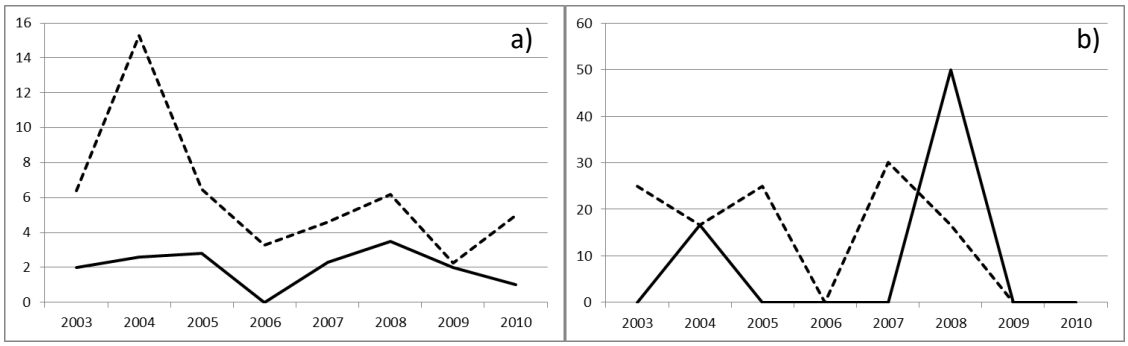


Figure 20. Group size a) and percentage of sightings with calves b) of harbour porpoise (black line) and bottlenose dolphin (dash line) per year.

Bottlenose dolphins are also present in coastal waters of Galicia. They were seen more often than porpoises (Table 13), with bigger group sizes, and more often with calves (Fig. 20 a, b). Porpoises were seen in deeper waters and not usually within the rías although this variation between depth zones in sighting rate of porpoises was not found to be significant ($\chi 2 = 6.19$, d.f. = 3) (Fig. 17 b, 18 b). .In contrast, bottlenose dolphins were seen mostly inside the rías although there are several records offshore, and the sighting rate differed significantly between depth classes ($\chi 2 = 105.13$, d.f. = 3, $p<0.001$). Bottlenose dolphins were seen in all the years of the study, with the highest number of sightings of this species in the first year with a second peak in 2006, when no porpoises were detected. While bottlenose dolphins were seen in all surveyed months but March, porpoises were not detected from March to May (Fig. 19 b, d) (there were no surveys during November to February).

Models and selection criteria.

Finally, from the three response variables defined (harbour porpoise presence, the group size and presence of calves) only the first one was analysed as most of the groups were of 1 individual and therefore the information was the same as that provide by the presence response variable; and there were very few records of sightings with calves and when they were detected only one calf was present.

At the data exploration stage, no outliers were detected, but some correlations between explanatory variables were detected. Due to collinearity several explanatory variables were dropped out: bearing, SST-STD, CHL-STD, DEP-STD and DEP_SL-STD. In most of these cases, means and standard deviations of variables tended to be correlated and we therefore retained mean values.

When modelling the effect of the environmental co-variables on the observers a total of 105 different candidate models was fitted (Appendix VI). The final model (where Y = porpoise presence) was the one with lowest AIC value and highest percentage of deviance explained. This model includes 3 explanatory variables:

Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) (AIC 279.06, Deviation Explained 13.3%).

The model shows a linear increase of sightings of harbour porpoises as the field width increases (edf = 1, P < 0.001, Fig. 21). In relation to vessel speed, porpoises were more frequently seen when speed increased to 6 knots, after which sighting frequency decreased as the speed increased (edf = 2.45, P < 0.001). There is a clear negative effect of wind strength, especially at Douglas values greater than 2.

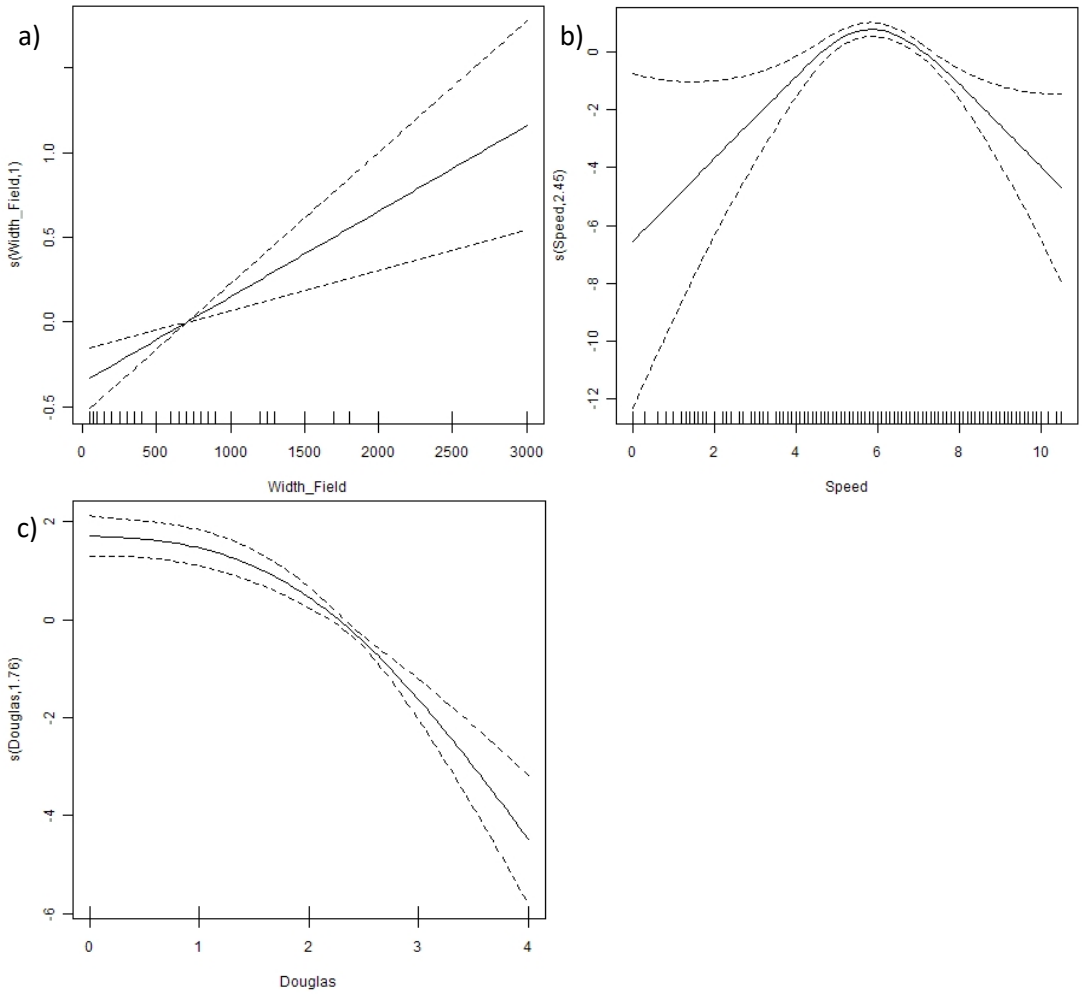


Figure 21. GAM results: smoothers showing partial effects of environment on the observers.

Covariates: a) field width (m), b) vessel speed (knots), c) Douglas.

To quantify the spatiotemporal trends in porpoise presence only one (full) model was fitted as all variables had a significant effect.

Y~ 1 + s(Year, k = 5) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(Month, k = 4) + s(Long, Lat) (AIC 270.89, Deviation Explained 28.3%).

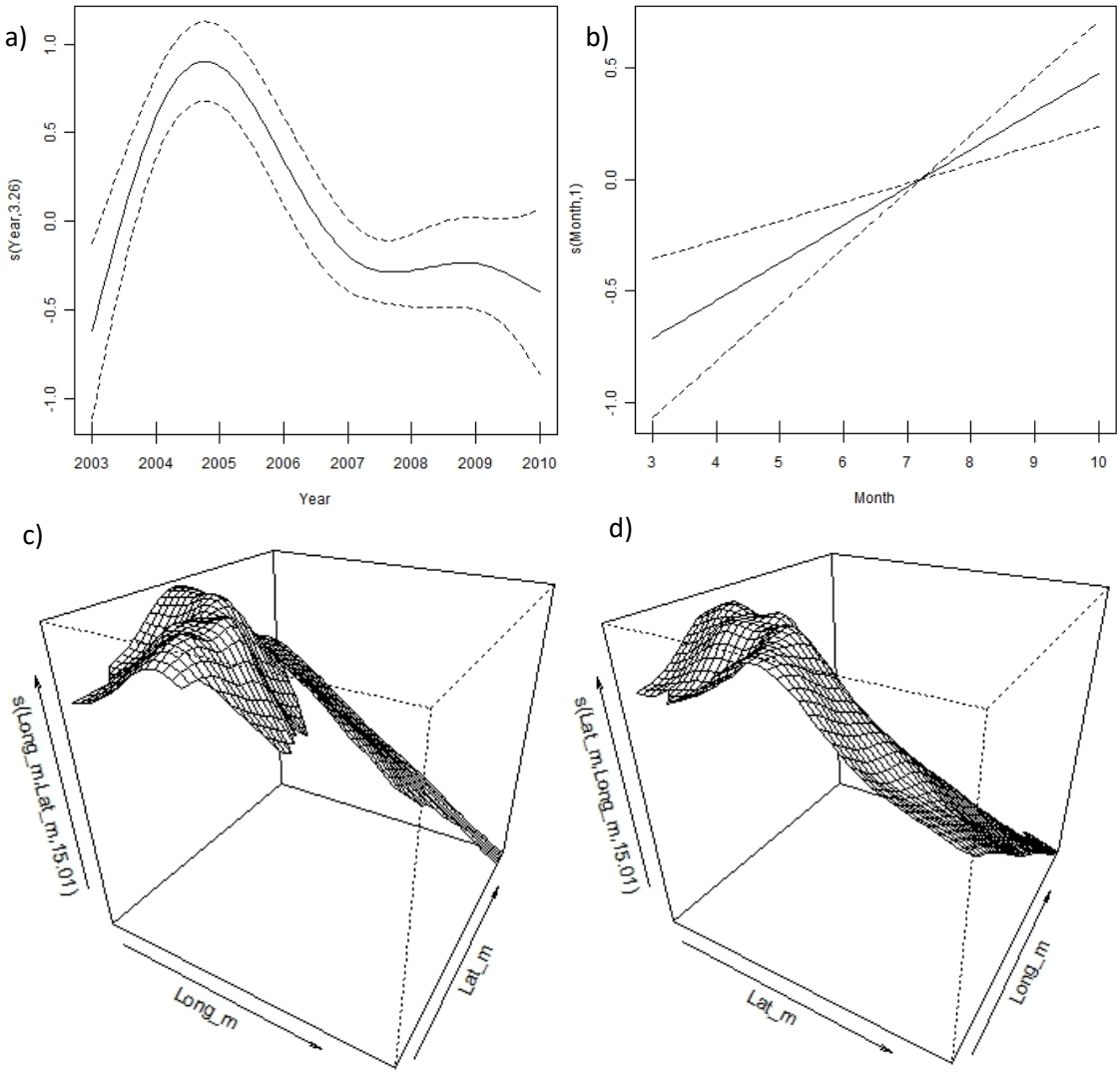


Figure 22. GAM results: smoothers showing partial effects of space and time. Covariates: a) year, b) month, c) latitude and longitude.

There is a significant year to year variation with a peak in 2005, although since 2007 the trend is not clear as the confidence intervals were wide (edf = 3.26, P < 0.001; Fig. 22 a). A positive trend was found in the sightings over the course of a year (edf = 1, P < 0.001; Fig. 22 b). The spatial effect on sightings when fitting latitude and longitude with an interaction (i.e. as a 2-dimensional smoother; Fig. 22 c, d) showed that there was a lower probability of detecting porpoises on the North coast of Galicia than on the South coast.

Then GAM models were fitted with habitat covariates in addition to the above variables. As the number of covariates was high, when a variable was not statistically significant it was dropped out. A total of 300 candidate models was fitted (Appendix VII y VIII); in this case there was not a unique best model and 3 models, where Y = porpoise presence, were selected (with very similar AIC):

model 1: Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4), 259.39 AIC, 25.6% of deviance explained;

model 2: Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4), 259.6 AIC, 24.8% deviance explained;

model 3: Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3), 259.9 AIC, 24% deviance explained.

The partial effects of these covariates are shown in Fig. 23; all variables have a linear effect except CHL and SST. Slope is present in all 3 selected models, showing a linear increase of sightings with an increase of the slope (edf = 1, P< 0.0001, for all models; Fig. 23 a); the smoother shown in this figure is not informative at slope values of less than 1.4 radians as confidence limits are very wide, reflecting lack of data. More porpoises were seen in areas where the CHL concentrations were lower ($edf_{1\text{-}2}$ = 2.03, edf_3 = 1.99, P < 0.0001; Fig. 23 b, c), but above a value of 15 Chl-a mg/m³ the confidence limits are wide due to lack of data. There was a positive effect of increasing ZEU value (edf = 1, P < 0.0001, for all models; Fig. 23 d). The incidence of sightings was greater at medium SST (edf_1 = 2.13, $edf_{2\text{-}3}$ = 2.14, P < 0.0001; Fig. 23 e, f). The probability of seeing porpoises is greater over seabeds facing South than over those facing North (DEP_ASP_cos, edf = 1, P < 0.001, for all models Fig. 23 g). In the first and second

models there is a linear positive effect of month, porpoises were seen more frequently in October than May, but this variable was not statistically significant in model three (edf = 1, P < 0.0001; Fig. 23 h). There is a linear increase of sightings with increasing ZEU_STD, but it is only significant in the first model (edf = 1, P < 0.001; Fig. 23 i).

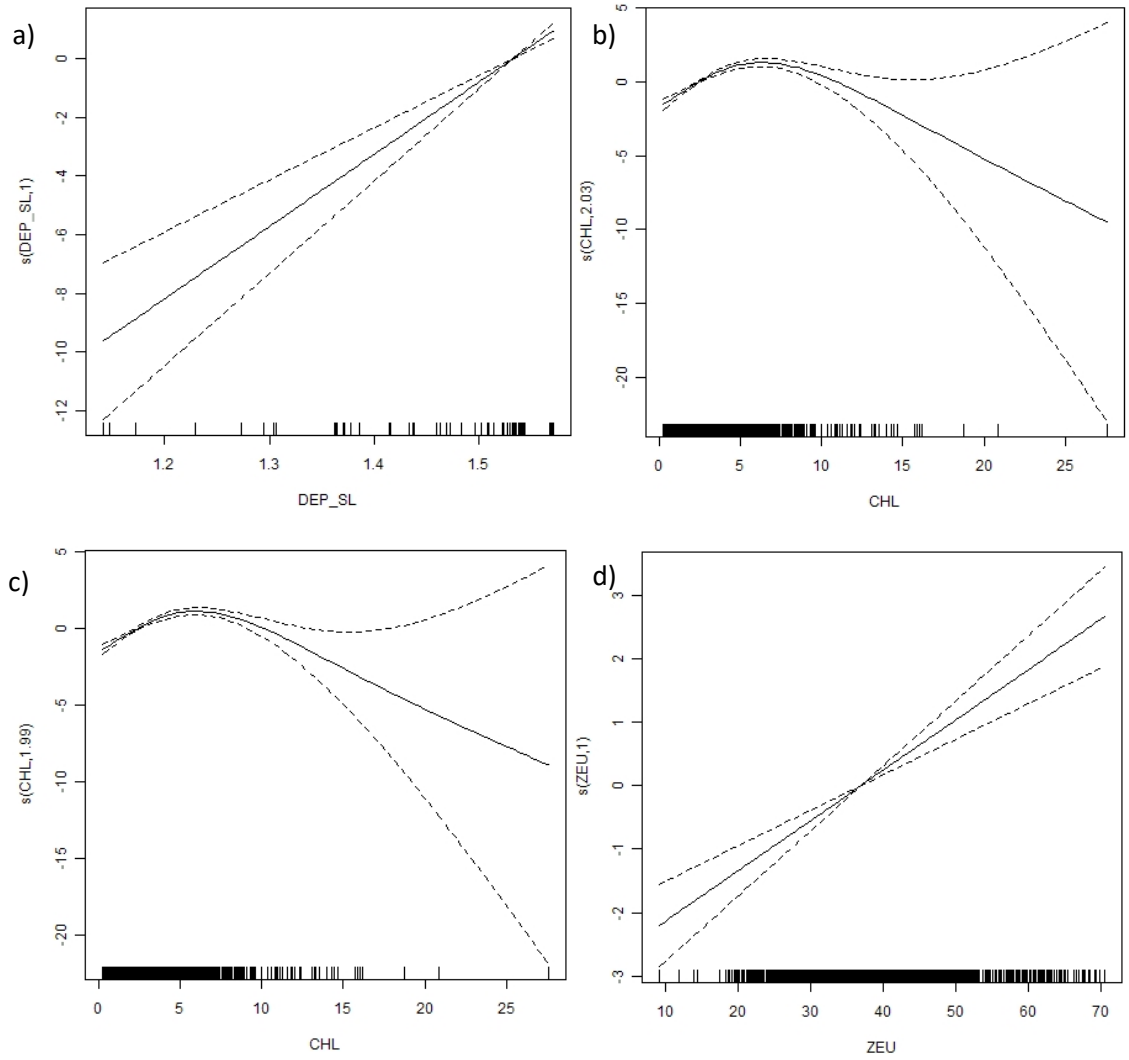


Figure 23. GAM results: smoothers showing partial effects of habitat covariates. a) seabed slope (rad), b) Chl-a (mg/m^2) for models 1 and 2, c) Chl-a (mg/m^2) for model 3, d) euphotic depth (m), e) sea surface temperature (ºC) for model 1, f) sea surface temperature (ºC) for models 2 and 3, g) depth aspect easting (rad); h) month; i) Euphotic Depth standar deviation.

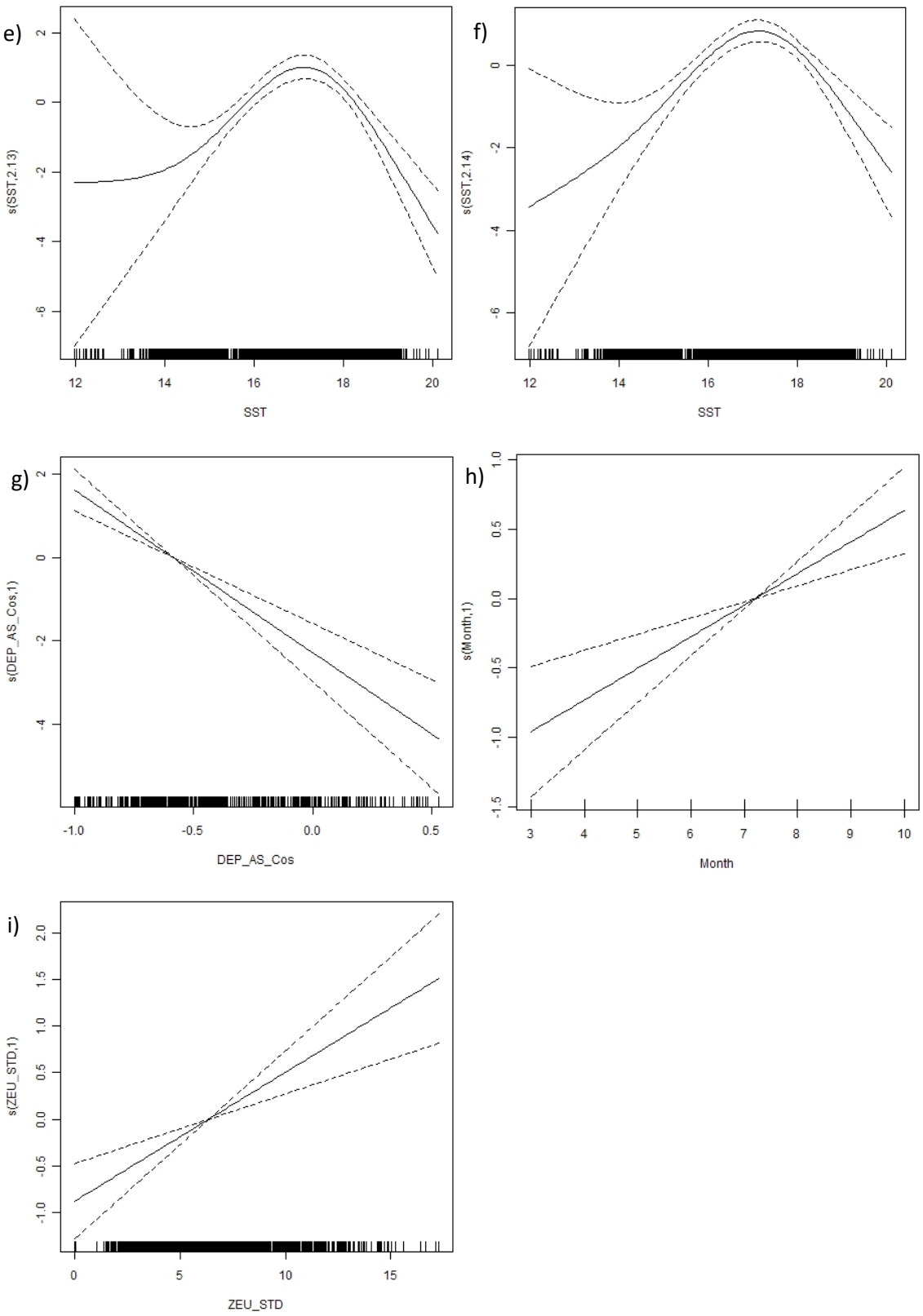


Figure 23 . Continued.

Discussion

The identification of the factors affecting the detection of porpoises by observers is fundamental and needs to be kept in mind when studying the environmental conditions that determine the presence of porpoises in the area. So-called “false absences” are a problem for cetacean sightings surveys, especially for harbour porpoises that have small size, are often solitary and have a cryptic surfacing behaviour, although spending nearly half of their life at or near the surface (Westgate et al 1995). As was described before by other authors, in this study the detection of porpoises was influenced by sea state (Palka 1996, Evans and Hammond 2004, Weir et al 2007, Tynan et al 2005, Marubini et al 2009, Embling et al 2010, Pierce et al 2010, Booth et al 2013, Dolman et al 2013, de Boer et al 2014), and it was found that the probability of detection decreases with values of Douglas greater than 2.

It was also found that the best boat speed for monitoring harbour porpoises is 6 knots. In other studies, in contrast, this variable was the only survey variable studied that did not have an effect on the sighting rates (Booth et at 2013) or was important but only for one year of study with a decrease of the detection rate for boat speed higher than 6 knots (Embling et al 2010). Sometimes porpoises appear to change their trajectory to swim away from boats (pers. obs.), thus it could be expected that at lower speeds more porpoises can be detected, but lower speeds might also allow porpoises to detect the ship and its trajectory earlier, and then avoid it more easily. On the other hand, at faster speeds the probability of detecting porpoises decreases as they spend only a short time at the surface which makes them difficult to detect. However, it should be noted that in large-scale cetacean surveys like SCANS, avoidance of vessels by porpoises has not been considered to be an issue (see Hammond et al 2002, 2013).

As was expected, the probability of detecting harbour porpoises increases with field width. The increase of the surface available to scan increases the probability of detect porpoises. However due to the difficulty to detect them, there is a distance from the boat at which this trend is no longer seen, for example, in Galicia it was calculated that only 45.8% on average of the porpoises were detected at 800 m from the boat (López et al 2012).

During the surveys carried out in Galician coastal waters, several environmental variables were found to be important to explain the presence of porpoises. Porpoises were mostly seen in waters with medium temperatures (between 16 – 18°C), a normal situation during summer in Galicia (Fraga 1981, Triñanes et al 1993, www.meteogalicia.es) when the Eastern North Atlantic Central Water (ENACW), a salty subtropical water mass is upwelled. However,

porpoises are described to be present mainly in colder waters (e.g. between 5 - 14°C; Evans and Teilmann 2009). The importance for the Iberian harbour porpoises of the temperature found here suggests that they are sensitive to temperature variation. It was suggested that climate change can affect the distribution of cetaceans such as harbour porpoises because of the predicted increase of water temperatures that may cause the species be found out of its thermal limits and then they cannot survive (e.g MacLeod et al 2005, Learmonth et al 2006, Laidre et al 2008, MacLeod 2009, Lambert et al 2011, 2014), especially in areas of distribution at the limit of their tolerance range (MacLeod 2009, Lambert et al 2014). Increase in water temperature in Galicia, which is near the southern limit of harbour porpoise distribution, may thus be of particular concern.

Other important variables were chlorophyll concentration and the depth of the eutrophic zone (depth where there is sufficient Photosynthetically Active Radiation (PAR) to support photosynthesis (Kirk 2011)), with an increase in porpoise presence as values of those variables increased. High chlorophyll conditions can be related to the upwelling conditions that are usual in the study area (e.g. Fraga 1981, Figueiras et al 2002, Álvarez et al 2005, 2010, 2012). The increase of nutrients in the water due to the upwelling of nutrient-rich waters leads to an increase in primary productivity and therefore the chlorophyll concentration. This will affect the secondary productivity and will lead to a higher presence of porpoise prey in the area. Previous work in the same area found that porpoises were present at a wider range of CHL_a concentrations than other species during summer (Fernández et al 2013). Also porpoises were seen most frequently adjacent to the coast in less productive areas (Pierce et al 2010) which may be a consequence of preferred water temperature and depth of the species and possibly of avoiding bottlenose dolphins (which were found in the most productive coastal areas). In the present study, the positive relationship found is consistent with studies in other areas such as California (Tynan et al 2005), Bay of Fundy (Johnston et al 2005) and the North Sea (Gilles et al 2011). The eutrophic zone has been used to describe the productivity of a water body; areas with larger eutrophic zones are more productive (Haande et al 2011, Jin et al 2011, Khanna et al 2009). Thus the results of the present study also suggest that porpoises were mostly detected in more productive areas.

All models showed a positive relationship between porpoise presence and both seabed slope and its facing to the South. Seabed slope has been found to influence porpoise distribution before (Embling et al 2010, Isojunno et al 2012, Booth et al 2013). This could be due to the presence of a slope current which is stronger and more persistent than shelf currents and has

an onslope tendency in mid depths (Pingree and Le Cann 1989). This slope current is generated by the interaction of a meridional density gradient with the slope and wind forcing with a poleward flow in the western boundary region (Gil 2003) below the surface (Huthnance et al 2002, Mason et al 2005) that in the Atlantic Iberian waters is favourable and increases the currents where sea bed faces the south and that often extends to the surface during winter, increasing the productivity of the area. In the study area, this current is known as the Iberian Poleward Current (IPC) (Peliz et al 2003) and the Portugal Coastal Counter Current (PCCC) (Ambar and Fiúza 1994). Often this poleward undercurrent causes the appearance of upwelling water, as happens in Galicia. The distance to the inshore edge of the upwelling front was one of the most important variables influencing the presence of porpoises in California (Tynan et al 2005). In the Horns Reef area (eastern North Sea), upwelling was described as the most important habitat characteristic for the distribution of porpoises that alternate between two upwelling cells depending on the direction of the tidal currents (Skov and Thomsen 2008). Also, in the German Bight, porpoises preferred areas with stronger currents and concentrated in areas where fronts are likely (Gilles et al 2011). Peliz et al (2003) confirmed that the adjustment of a meridional density gradient to a meridional oriented slope is likely to be the central mechanism in the generation of IPC, that together with the topography creates surface features such as eddies along the slope. It has been found that total primary production related to the "Canary Eddy Corridor" may be as high as the total production of the northwest African upwelling system for the same latitude (Dower and Perry 2001) which may be important sources of food for another fish, marine mammal, cephalopods and birds.

These results show that porpoises are likely related to areas with conditions of high productivity as was described before (e.g. Tynan et al 2005, Gilles et al 2011). These conditions will ultimately affect the higher trophic levels through food chain-related processes, and therefore highly productive areas of upwelling or eddies may be good for the development and aggregation of the most important prey of harbour porpoises in Galicia such as blue whiting, *Trisopterus* spp, silvery pout (*Gadiculus argenteus*) and *Trachurus* sp. (Pierce et al 2010, Read et al 2012) that can be found on the continental slope (blue whiting) and the shelf waters (the other species). Remaining close to food resources, porpoises are able to meet the energetic demands of maintenance, growth and reproduction, which are relatively high, especially in the case of mature females which have the additional costs of pregnancy and lactation that increase energy demands and may happen at the same time (Brodie 1995, Kastelein et al 1997, Read and Westgate 1997, Read et al 1997, Koopman, 1998, Lockyer 2007, MacLeod et al 2007). Then their distribution is likely to reflect foraging opportunities.

There was also variation in the number of porpoise sightings with year and season. The interannual variation showed a significant increase in the number of sightings in 2005 and no detections in 2006. Results from land-based surveys in Galicia (Pierce et al 2010, Chapter III) showed also interannual variation, but with peaks in different years. This variation in porpoise presence may be due to the survey of different areas (i.e. in relation to depth and proximity to the coast) with both techniques, so in some years porpoises could be closer to the coast so they will be detected better with coast surveys than boat surveys, and *vice versa*. Variation between years was also found in other areas of Europe, such as Scotland (Marubini et al 2009, Booth et al 2013) and the Baltic Sea (Benke et al 2014). Benke et al (2014) suggested that those differences in the Baltic Sea could rather indicate a change in site or habitat preference than a population increase. Similarly, in Galicia, it is unlikely that the changes in sightings rates from year to year reflect absolute abundance. It is possible that in Galicia the changes in porpoise distribution over the years reflect the use of different areas during the study period due to changes in prey distribution or abundance, or movement of porpoises from deeper to coastal waters between years.

Seasonal variation has been documented with an increase in the number of sightings in summer also in other areas (Siebert et al 2006, Verfuβ et al 2007, Weir et al 2007, Gilles et al 2011, Booth et al 2013, Benke et al 2014), maybe partly due to better weather conditions that make it easier to detect the porpoises. However there are also differences in the seasonal patterns in local abundance between areas. For example, in Scotland more porpoises were detected in summer (Booth et al 2013), in German North Sea in spring (Gilles et al 2009), the Netherlands in winter (Camphuysen 2004, 2011, Scheidat et al 2011) or within different areas of Ireland (Berrow et al 2014). The reasons for those differences between seasons are not clear. One explanation could be the differences in the distribution through the depth classes, with animals moving from deep to shallow waters and *vice versa*.

In Galicia, there were no significant differences in porpoise presence between months or in relation to depth although porpoises were seen in deeper waters. Other possible reasons for the variation in the number of sightings of porpoises in the study area could include the reduction or movements of prey available for porpoises. In the study area, fish landings and recruitment in the Bay of Biscay and Atlantic Iberian waters did not show any evidence of reduced abundance during the study period for the species eaten by porpoises in the area (ICES 2012), although there could be differences on a more local scale.

The use of habitat modelling techniques gives the possibility to increase our knowledge of the porpoises of Galician waters. Then the environmental conditions and areas in which porpoises were seen with higher probability will be better known and suitable areas for their conservation can be established with more accuracy. The modification of those habitat conditions favourable for porpoises may affect the presence and survival of porpoises, so it will be necessary to detect and consider the most important threats in the conservation plan and the actions to maintain the porpoise population.

While the association with high productivity may help to define preferred areas, in a mobile species it is also essential to take into account variation in distribution, not only seasonal but from year to year. For example, if the conservation objective is to establish protected areas it is necessary to be reasonably certain that porpoises will continue to use the same areas every year – and if this is not the case a more flexible system of spatial protection may be needed, one which can be adapted to changing distributions.

In the current study the best models explain around 25% of the deviance (13% due to the variables that affect the observers and 13% due to environmental variables). While explaining all variation in distribution may be an unrealistic goal (links between environment, fish and porpoises are probably intrinsically variable), further work could help to improve the models and their utility. For example,

i. increasing the boat-survey effort with surveys all year around, along the whole Galician coast, reaching deeper areas, and keeping them in time;
ii. studying the effects of more variables that may affect the presence of porpoises such as tide, traffic of boats or fisheries information; or,
iii. identifying areas where calving takes place and calves are reared as well as feeding areas. Visual observation may be insufficient for this and other possibilities should be considered, such as attaching time-depth recorder tags to record movements and behaviour,
iv. complementing the results of different methodologies (land-based surveys, diet, genetics, acoustics).

CHAPTER IV

Presence of harbour porpoise and habitat preference in Galician waters from land-based survey data.

Ángela LLavona, Pablo Covelo, Juan I. Díaz, Mara Caldas, Jose A. Martínez-Cedeira, Alfredo López, Vasilis Valavanis, José V. Vingada and Graham J. Pierce.

Conceived and designed surveys and sampling: JAM-C, AL, GJP.

Collected the data: ALL, PC, JID, MC, JAM-C, AL

Designed the analysis: GJP and ALL

Analyzed the data: ALL.

Contributed materials/analysis tools: AL, VV, GJP.

Wrote the paper: ALL.

Edited the text: GJP.

Provided constructive comments on the manuscript and approved the final document: GJP, AL, JVV.

Abstract

The Galician coastline is around 1195 km long, with a series of drowned valleys “Rías” along the west coast and an easy access to most of the coast, and is thus a good area to carry out land-based survey which is a method used for studying different species of cetaceans in different areas. This method has several advantages such as the low cost, the opportunity to survey every day of the year, the prevention of under- or overestimation of sightings due to the response of the animals to the boat, by avoidance or attraction. However, the study of cetaceans from the coast is limited by the restriction of monitoring to only those areas visible from the coast, and information that requires close proximity to animals is hard to collect. In addition, it is known that cetacean distribution is related to sea depth, therefore only the more coastal species can be studied.

Data were collected by the NGO CEMMA (Coordinadora para o Estudo dos Mamíferos MAriños) from 2003 to 2011 by systematic monthly surveys from a series of observation points along the Galician coast to cover the study area as evenly as possible.

Generalized Additive Models were used to study the effect of several environment covariates. But first, factors that can have some influence on the detection of cetaceans by observers were analysed. This is especially important for harbour porpoises which are difficult to detect visually. In the present study five variables were found to have some influence on the observers in relation to the detection of porpoises: i) the duration of the observation; the more time that the observers have available to search for porpoises at the station, the higher the probability of detecting them if they are present in the area. To avoid a decrease in the efficiency of the search due to the fatigue of the observers there is also a maximum of the duration of the observation period, which in the current study begins approximately at 100 minutes. ii) The area available for survey (i.e. the field of view): in larger areas the probability of porpoise detection increases but also if it is too big the observers will probably not scan all the area with the same effectiveness and detection probability would be expected to reach an asymptote. iii) The sea state, which had an important influence on the (apparent) presence of porpoises. And, iv) the presence of bottlenose dolphins, being negatively correlated with detection of porpoises, and may be not only due to the effect on the observer but on porpoises themself.

Taking into account those variables, there was a temporal trend during the study period, with an increase in the number of sightings over the years, which could be due to a change in the

distribution of the population or a growth of the population, but this last explanation does not seem to be possible with the life history knowledge of the harbour porpoise in the study area. Also, a temporal trend during the day and a spatial trend were found. There was an increase in the number of sightings later in the day, and the number of sightings increased northwards with more detections in Lugo and A Coruña (Northern stations).

In relation to environmental variables likely to affect porpoise distribution, the depth of the eutrophic zone (ZEU) was significant in the models fitted, with the highest values of ZEU indicate areas of high productivity. In addition, more porpoises were detected in waters where depth was more variable, sea bed slope was greater and the continental shelf was narrower. This highlights the importance of high productive areas, and areas where the shelf is narrower, which could be related to the diet of porpoises as the principal prey varies between areas.

However it is not only "natural" conditions that seem to determine the distribution of porpoises. Porpoises were not detected inside the Rías, which are mostly located along the West and Southern coast of Galicia, and are more industrialized and where most bottlenose dolphin sightings occur. Although it is difficult to demonstrate cause and effect, since environmental differences, presence of bottlenose dolphins and anthropogenic impacts are potentially confounded, areas with higher human population density were those with lower probabilities of detecting porpoises.

In Spain, although the Habitats Directive requires the Member States to create Special Areas of Conservation (SACs), no SAC has been established specifically for harbour porpoises, although some of the SACs consider its presence. The results of this study provide essential information about this species in Galicia, which is important to keep in mind. For example, i) protected areas cannot be seasonal; ii) one of the key areas in the Iberian peninsula is Galicia, as is maybe also the case for the Gulf of Cadiz (Consejería de Medio Ambiente y Ordenación del Territorio 2015), with particularly high occurrence of porpoises around Punta Candieira, Vilán and Touriñán Cape, Punta Remedios (Lira) and Faro de Corrubedo; iii) the same SAC is not going to be useful for both harbour porpoises and bottlenose dolphins, as the main areas used by them are different and populations do not seem to behave in the same way; a large reserve might be suitable for both species, but only if it is big enough to cover those different areas required by each.

Introduction

Marine ecosystems are protected by the Habitats Directive, under which one conservation tool is the creation of SACs by the Member States. The harbour porpoise (*Phocoena phocoena*) is included in Annex-II of the Habitats Directive, requiring the designation of SACs. Together with the other necessary conservation measures, those protected areas should help to maintain (or restore) the favourable conservation status of the natural habitats and/or populations of the species for which the site had been designated, prohibiting deterioration or destruction of breeding sites or resting places (Article 12), and avoiding their disturbance (Article 6) particularly during the period of breeding and migration (Article 12). In adition, the harbour porpoise is designated as ”vulnerable” in Spain (Catálogo Nacional de Especies Amenazadas, Law 4/1989, 2000).

Moreover, the study of porpoise populations is a priority issue worldwide: IWC (International Whaling Commission) and ICES (International Council for the Exploration of the Sea) recommended studies to determine the population structure of this species and develop an appropriate management plan (IWC 1998) in order to reduce negative impacts on their populations.

The population of harbour porpoises in Galician waters has been described as genetically isolated from the rest of the North East Atlantic (Fontaine et al 2007, 2014, see also Chapter II), is known to be present all year around (Lopez et al 2002, López 2003, Pierce et al 2010) and seems to be a coastal species, although it needs to be confirmed by more surveys at deeper areas (López et al 2002, Pierce et al 2010, Spyrakos et al 2011, Fernández et al 2013, Méndez-Fernandez et al 2013, 2014 a, b). Their abundance has been estimated to be 974 (CV=0.84) individuals in an area extending from SW France, along the Atlantic coast of Spain and Portugal (Hammond et al 2013); of 683 porpoises (CV=0.63) in Galicia and Cantabria (López et al 2013), and of 386 porpoises (CV= 0.71) in Galicia (López et al 2012). The first of these estimates derives from the SCANS-II survey in July 2005 while the latter are based on several and independent surveys in the period of 2003 - 2011 in North Spain.

The Galician coastline is around 1195 km long, with a series of drowned valleys (“Rías”) along the west coast, and a narrow continental shelf with a maximum width of 80 km at A Coruña (Cabanas 1999). Galicia is located at the northern limit of the NW African upwelling system, which produces an enrichment that favours biological production (Cabanas 1999), and helps make Galicia the main fishing region of Spain and one of the most important in the world. Its

topography and the location of 58% of Galician population at the coast contribute to have an easy access to most of the coast, and makes the land-based survey method to study cetaceans a good choice.

Land-based survey is a method used for studying different species of cetaceans in different areas (e.g. Goodwin 2008, Pierce et al 2010, Dolman et al 2013, Arranz et al 2014). Comparing with boat-surveys, it is a method with relatively low costs and it is easier to access the entire coast than it is by boat surveys, as observers can travel to stations by car or even walking. Another advantage is the opportunity to survey every day of the year, which is not always possible with boat-surveys, as days-at-sea are usually limited to some period of the year due to economic, weather or logistic reasons. Also the under- or overestimation of sightings due to the response of the animals to the boat, both by avoidance and attraction (e.g. Williams et al 2002 a, b, 2004, Scheidat et al 2004, Lusseau 2006, Christiansen et al 2010), is prevented. However, the study of cetaceans from the coast is limited by the restriction of monitoring to only those areas visible from the coast, and information that requires close proximity to animals is hard to collect. In addition, it is known that cetacean distribution is related to sea depth (Caretta et al 2001, Cañadas et al 2003, Santora 2012); therefore only the more coastal species can be studied.

Data recorded by this method are effective to study temporal and spatial trends with accuracy and provide standardized, effort-based information on species presence and relative abundance in coastal waters (Evans and Hammond 2004). Although studies such as the one carried out by Dolman et al (2013) obtained comparable densities of harbour porpoise and minke whales (*Balaenoptera acutorostrata*) from boat and land-based surveys, it is important to keep in mind that the occurrence of animals is monitored in a particular restricted area and not the population at large, and if broader geographical coverage is required, it may be advantageous to combine monitoring from fixed stations with offshore line transects (Evans and Hammond 2004).

Cetacean data obtained can be used in habitat modelling, a potentially powerful tool for predicting cetacean distributions and understanding the ecological processes determining these distributions, which has already been used to incorporate this variability into monitoring programmes and management measures, including improvement of abundance estimates, development of marine protected areas, and understanding cetacean–fisheries interactions (Redfern et al 2006).

In 2003 systematic monthly surveys were established by the NGO CEMMA (Coordinadora para o Estudo dos Mamíferos MAriños) along the Galician coast. Pierce et al (2010) found that the most frequently recorded species from the coast during 2003 - 2007 were the bottlenose dolphin (*Tursiops truncatus*), common dolphin (*Delphinus delphis*), harbour porpoise, Risso's dolphin (*Grampus griseus*) and long-finned pilot whale (*Globicephala melas*), each with different distribution patterns along the coast (see also López 2003, Lopez et al 2004, Fernández 2010, Pierce et al 2010, Spyrakos et al 2011, Méndez-Fernandez et al 2013, Fernández et al 2013). The land-based data collection continued until 2013. Here we consider data up to 2011, as well as using several additional environmental variables not considered in the earlier study, with the aim of focusing on harbour porpoise to study i) seasonal and ii) temporal trends in harbour porpoise distribution in the study area, iii) to compare its distribution with that of the bottlenose dolphin, iv) to study the environmental characteristics of the habitat where harbour porpoises are present and compare them with previous studies of the habitat use by cetaceans of that area (Fernández 2010, Pierce et al 2010, Spyrakos et al 2011, Méndez-Fernandez et al 2013, Fernández et al 2013).

The information about harbour porpoise in Galicia obtained can be used for the development of a management plan, including the establishment of SACs. Moreover, together with other ongoing and previous studies (boat surveys, strandings, by-catch), it will help to evaluate the status of porpoises, as part of the evaluation of "good environmental status" (GES) in Galician waters as required by EU regulations as required by the Marine Strategy Framework Directive.

Materials and methods

Study area.

The Galician coastline has a length of around 1195 km with cliffs, sandy beaches, and a series of "rías", which are flooded tectonic valleys of moderate depth. At the mouths of the Rías Baixas (Rías of Vigo, Pontevedra and Arousa, in south Galicia) there are the archipelagos of Cíes and Ons, and Sálvora Island. The narrow continental shelf of Galicia (mostly 20 - 35 km wide, with a maximum of 80 km) is influenced by seasonal upwelling (Fraga 1981) caused by northerly winds, during spring and summer, and Ekman transport. This oceanographic process is important especially due to the associated enrichment, which favours biological production (Cabanas 1999) and makes Galicia the main fishing region of Spain and one of the most important in the world, and the region with, for example, the highest mussel (*Mytilus galloprovincialis*) production in the world on floating rafts. In total, 22 cetacean species have been recorded in this area (Piñeiro-Seage 1989, López et al 2003, Covelo et al 2009, 2015).

Survey design and data collection.

In 2003, CEMMA searched the Galician coastline to identify optimal observation stations / points (OP) for the systematic survey of the entire coast for the study of cetaceans. The OP must afford a good view of the sea, be high enough to allow observation of a large area of sea but not so high as to decrease the detectability of small species present in the study area such as the harbour porpoise, and offer easy accessibility for the observers.

In total 54 OP were selected and are shown in Fig. 24 and Appendix IX a, b. It was not possible to establish stations on the Islands due to the difficulty of transport in autumn and winter, although some observations were made from the islands, for example on Ons (at Burato do Inferno) in 2007.

For each OP, latitude and longitude are known (Appendix IX a, b). Because of logistic and financial reasons, an analysis of the efficiency of the OP coverage was carried out and found that the number of stations could be reduced to 30 without the decreasing the ability of the survey to detect trends (Pierce et al 2010), therefore for the study of temporal and spatial trends only data from these 30 OP from 2003 to 2011 were used (Appendix IX a).

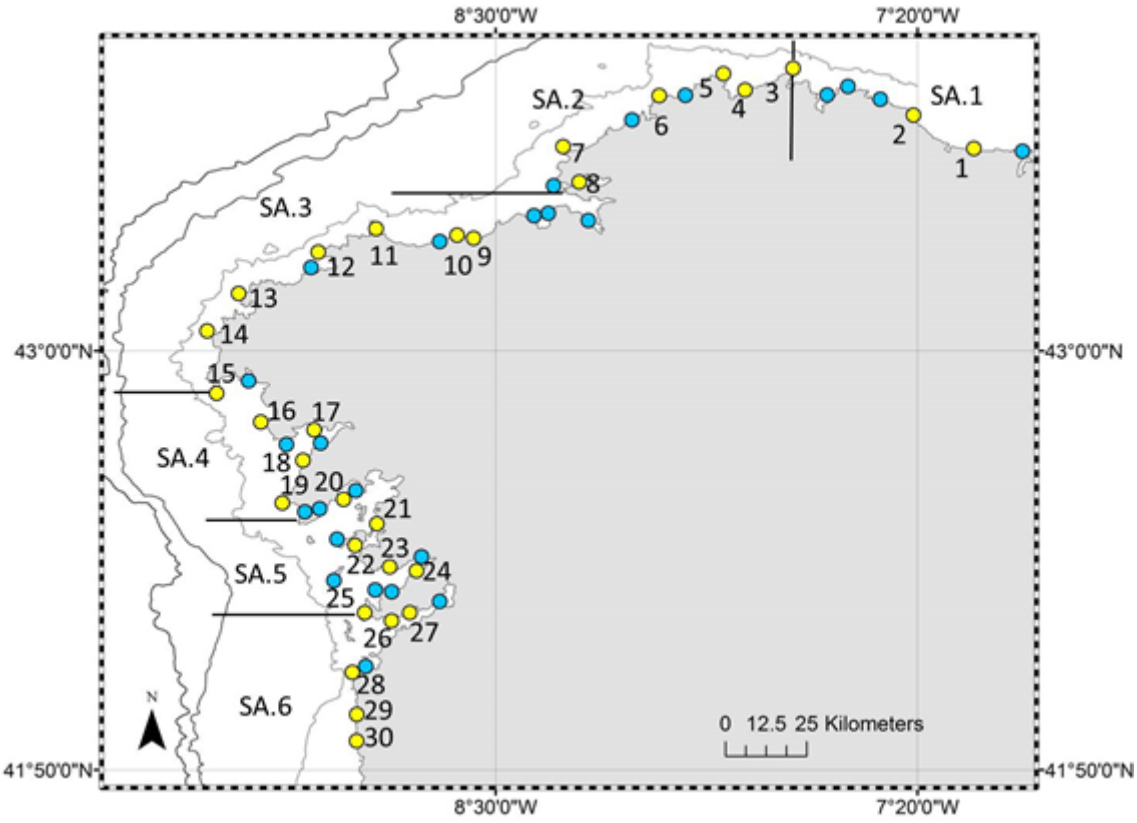


Figure 24. Positions of the observation points along the coast of Galicia. Yellow dots are the 30 points at which observation was carried out from 2003 to 2011; blue dots are observation points at which effort was also done from 2003 to 2007. Depth contours of 100, 200 and 500 m are represented.

Each OP was visited at least once during every month, usually by 2 observers (ranging from 1 to (very rarely) 9) who scanned the sea continuously with naked eyes, or using binoculars or telescopes. The duration of observations averaged 38 min (ranging 5 – 215 min; Fig. 25).

The data collected during each observation period included date, observation station, time at which observation started and finished, observer identity and optics used (binoculars only, telescope only, binoculars and telescope, none). Also some environmental data were collected: wind strength (Beaufort scale) and direction, sea state (Douglas scale), visibility (ranging from 0: dense fog, to 5: visibility of more than 10 miles) and estimates of the depth of field of view and the angle describing the field of view. The area covered by each observation at each OP was calculated from the last two parameters.

Data recorded for each sighting were: the time at which animals were detected, duration of the observation, estimates of the distance from the observer to the animals, angle (in relation to North), species, group size, type of group (compact, dispersed, mixed) and behaviour

(swimming (direction of travelling), resting, feeding, jumping, interactions with other species or boats).

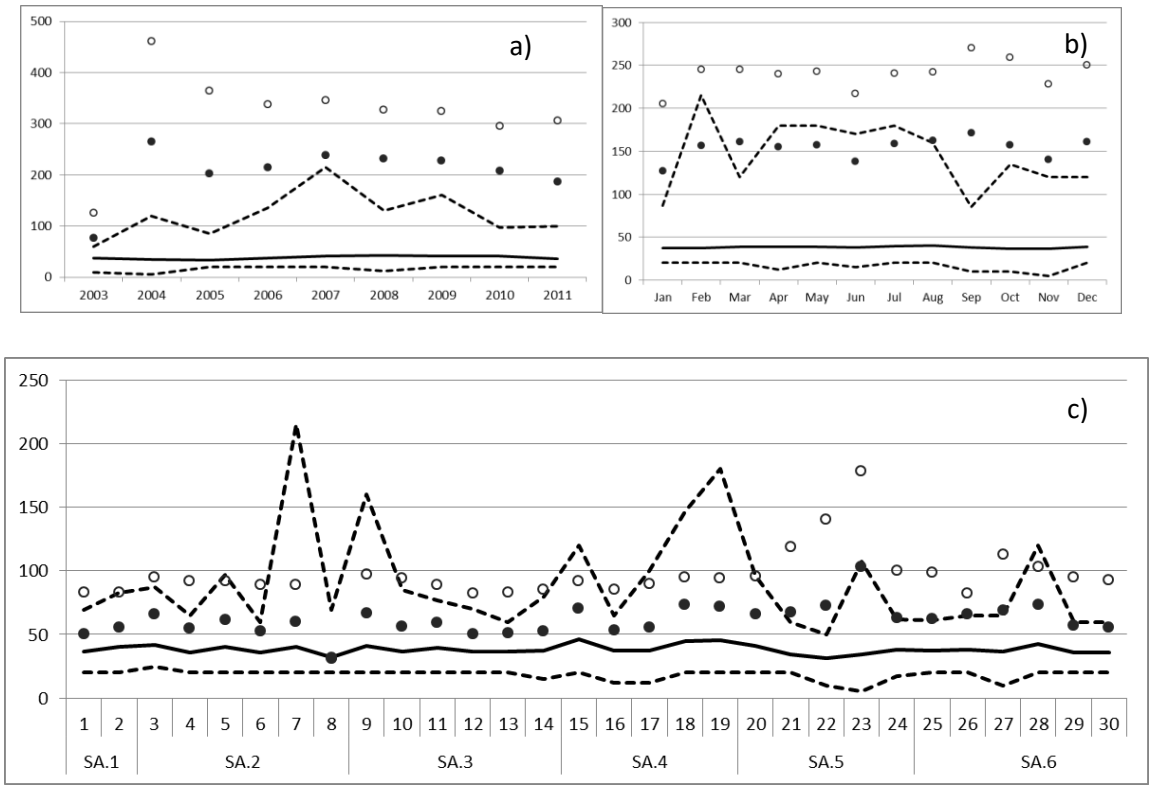


Figure 25. Duration of the observation periods in hours from coastal surveys at 30 Observation Points a) per year, b) per month, c) per observation point. In each case, the mean value is represented by a black line, and maximum and minimum values are shown as dashed lines. Total number of hours at each one is shown as black dots. Total number of periods of observation is shown as white dots. Number of hours per year, month and Observation Point is shown In Appendix IX.

Environmental data.

For the analysis of habitat use, a number of potential explanatory variables were considered: sea surface temperature (SST), chlorophyll concentration (CHL), euphotic depth (ZEU), photosynthetically active radiation (PAR), depth (DEP), seabed slope (DEP_SL), seabed aspect (DEP-ASP, that was separated into south-north and east-west components, using the sine and cosine, DEP-ASP-sin, DEP-ASP-cos), their standard deviations (SST-STD, CHL-STD, ZEU-STD, PAR-STD, DEP-STD, DEP_SL-STD, DEP-AS-STD) and, the distance from the OP to the 200 m isobaths (Dist_200m).

The study area is well monitored in terms of monthly satellite imagery. MODISA (Moderate Resolution Imaging Spectroradiometer Aqua at 4 km spatial resolution Level-3 datasets) sea surface temperature distribution (SST in ^{o}C), sea surface chlorophyll concentration (CHL in mg/m^{3}), photosynthetically active radiation (PAR in Einstein/m2/day), and euphotic depth (ZEU in meters) were downloaded through Oceancolor Web, NASA's online Distributed Active Archive Center. These monthly satellite datasets were downloaded in HDF (Hierarchical Data Format) and converted to ArcGIS grids through specific routines developed in AML (Arc Macro Language) for the workstation version of ArcGIS (ArcInfo). Bathymetry (DEP in meters at 800 m spatial resolution) was downloaded from GEBCO_08 (General Bathymetric Chart of the Oceans) and bathymetry slope (SLO) and aspect (ASP) were calculated in radians by applying the corresponding Z factor for the average latitude of the study area. Mean environmental and bathymetry parameters were calculated for each sampling point using a buffer zone of 20 km around each point. The procedure was carried out in the workstation version of ArcGIS using the grid zonal function 'zonalstats' for calculating mean and standard deviation (zonalstats function with the {moment} argument). Dist_200m was the distance from the OP to the 200 m isobath and was calculated using the ArcInfo workstation 8.0.2 NEAR function. The 200 m isobath was derived from GEBCO (www.gebco.net).

In addition, the human population index (POP) was included as a possible indicator of disturbance experienced by porpoises, and was calculated using Gridded Population of the World Version 3 (GPWv3), with a raster data are at 2.5 arc-minutes resolution and a buffer of 200 km.

Statistical analysis.

To analyse the significance of the variation of the sighting rates between SA, years and months, effects of year-SA and season-SA interactions were evaluated using a Chi-squared test. They were also carried out for group size, as groups with more than 4 individuals were a few, 4 groups were created: 1 individual, 2 individuals, 3 individuals and 4 individuals or more.

The Zuur et al (2010) protocol of eight steps for data exploration was followed to minimise type I and type II errors, although some violations of assumptions have little impact on the results or ecological conclusions (Zuur et al 2010). Those steps are: 1 - detection of outliers in response (Y) and explanatory (X) variables; 2 - study the homogeneity of y; 3 - study the normality of y; 4 - investigate “zero trouble” (i.e. zero inflation) in Y; 5 - study the collinearity of

different X; 6 - study the relationship between Y and X; 7 - search for interactions; and 8 - study the independence of Y (i.e., autocorrelation).

For the data exploration, boxplots, conditional boxplot and Cleveland dotplot / Dotcharts were plotted and correlations and Variance Inflation Factors (VIF) were calculated. As the response variables were binomial, no histograms or QQ plots were created. The result was that several of the explanatory variables had to be removed due to the presence of correlation with other covariates: DEP, SLO-STD and POP. Also the Easting component was removed as it was strongly correlated with the Northing component (presumably a consequence of the shape of the coastline) (Zuur et al 2007).

Harbour porpoise presence was considered as the response variable.

A three-step modelling process was used. Variables that could affect the detection of the harbour porpoises by the observers were firstly studied. Those variables were: number of observers, height of the OP, optics used, wind strength (Beaufort scale) and direction (Northing component), sea state (Douglas scale), visibility, area surveyed, duration of the observation and presence of bottlenose dolphins.

The final stage 1 model was used as the base for two further models, one model (stage 2A) containing spatial and temporal covariates, which aims to describe spatiotemporal variation in cetacean presence, and another one (stage 2B) including environmental covariates, which attempts to explain spatiotemporal variation. For model 2A, the covariates studied were: observation point, day of the year, year, time at which observation started. Observation point is used as a proxy for latitude and longitude, treating the coastline as a linear feature. For model 2B, covariates were: SST, SST-STD, CHL, CHL-STD, ZEU, ZEU-STD, PAR, PAR-STD, DEP-STD, SLO, DEP-ASP-sin, DEP-ASP-cos, ASP-STD, POP-STD, Dist_200m).

Generalised additive models (GAMs) permit non-normal distributions of response variables (including binary, discrete or continuous variables) and non-linear relationships between continuous covariates and the response variable, which are described with non-linear smooth functions (Hastie and Tibsshirani 1990). These models have been described as suitable to capture non-linear cetacean-habitat relationships (Redfern et al 2006). Therefore, they were used in this study to relate the presence of harbour porpoise to spatial, temporal and environmental covariates.

The distribution selected for the response variable was binomial (presence/absence data) and a logit link function was used. Covariates were fitted as smoothers except for year, which had

too few unique values. Degrees of freedom (k) were limited to permit to fit a smooth curve for variables with few values (e.g. Douglas) and to avoid overfitting or fitting unrealistically complex relationships (Zuur et al 2007) for environmental variables. Thus k=3 was used for covariates affecting the observers and the OP which have few different values and k=4 for spatial temporal and environmental covariates.

For the model selection the protocol of forwards selection was followed. The main criterion for the model selection followed was the Akaike's Information Criterion (AIC) and the percentage deviance explained by the set of explanatory variables in the model. In addition, where the AIC was uninformative about whether it was necessary to add an additional variable (e.g. AIC values differed by less than 2), F tests were used to compare nested models. Final best models were validated using plots of residuals versus fitted values to check for patterns and for homogeneity.

All these analyses were done using the software R.2.11.1 and Brodgar 2.7.2 (www.brodgar.com).

Results

Effort and sightings.

From 2003 to 2011 a total of 2325.8 h of effort was completed. As explained in the material and methods, from 2006 onwards not all of the original 54 Observation Points (or Stations, OP) were visited. Therefore all results presented correspond to the 30 Observation Points that were visited every year from 2003 to 2011 (Appendix IX, Fig. 24). This represents a total of 1847.95 h of observation; the distribution of observation effort by stations and year or month is shown in Appendix X. The study started in September 2003; thus this year has fewer hours of observation. Comparing across years and between months, the total duration of observations was lowest in 2003 (77.27 h) and in January (131.75 h), and was highest in 2004 (242.10 h) and in September (190.50 h). Mean values of the duration of the observations for each visit at each year, month and Station are shown in Fig. 25. There were differences between minimum and maximum number of hours of observation at different observation points. Observation duration ranged from 5 min to 215 min, with an overall mean value of 37.98 minutes.

A total of 671 sightings of cetaceans was recorded (Table 14), with an overall encounter rate of 0.363 animals per hour for all species. The most commonly sighted species of cetacean recorded were bottlenose dolphin (*Tursiops truncatus*) (54.8% of sightings) common dolphin (*Delphinus delphis*) (21.8%), and harbour porpoise (*Phocoena phocoena*) (12.4%). Other species observed were long-finned pilot whale (*Globicephala melas*), Risso's dolphin (*Grampus griseus*), fin whale (*Balaenoptera physalus*) and minke whale (*Balaenoptera acutorostrata*) (Table 14 a). Years 2004 and 2008 were the ones with most sightings (n=98 each year). If these data are considered per hour of observation (ER; Table 14 b), bottlenose dolphin remains the most commonly sighted species, followed by common dolphin and harbour porpoise. In contrast, it can be seen that there is not much difference between years, with the highest ER at 2008 in 2011, although from 2004 to 2007 and 2009 values were enough to be statistically significant ($\chi 2 = 45.86$, d.f.= 8, $p<0.001$).

a)

SPECIES	2003	2004	2005	2006	2007	2008	2009	2010	2011	TOTAL	% TOTAL
Tursiops truncatus	13	40	41	45	58	52	43	30	46	368	54.8
Delphinus delphis	4	34	18	19	15	19	10	15	12	146	21.8
Phocoena phocoena	0	9	12	12	3	13	13	6	15	83	12.4
Globicephala melas	0	4	0	2	0	1	2	1	2	12	1.8
Grampus griseus	1	1	2	2	2	0	1	1	1	11	1.6
Balaenoptera physalus	0	0	0	0	2	1	0	0	0	3	0.4
Balaenoptera acutorostrata	0	0	0	0	0	0	2	0	0	2	0.3
Unidentified delphinid	0	8	2	2	6	10	8	2	0	38	5.7
Unidentified mysticetes	0	1	1	1	1	1	0	0	1	6	0.9
Unidentified cetacean	0	1	0	0	0	1	0	0	0	2	0.3
TOTAL	**18**	**98**	**76**	**83**	**87**	**98**	**79**	**55**	**77**	**671**	**100**

b)

SPECIES	2003	2004	2005	2006	2007	2008	2009	2010	2011	TOTAL
Tursiops truncatus	0.169	0.151	0.203	0.210	0.244	0.225	0.189	0.145	0.247	0.199
Delphinus delphis	0.052	0.129	0.089	0.089	0.063	0.082	0.044	0.072	0.064	0.079
Phocoena phocoena	0	0.034	0.059	0.056	0.013	0.056	0.057	0.029	0.081	0.045
Globicephala melas	0	0.015	0	0.009	0	0.004	0.009	0.005	0.011	0.006
Grampus griseus	0.013	0.004	0.010	0.009	0.008	0	0.004	0.005	0.005	0.006
Balaenoptera physalus	0	0	0	0	0.008	0.004	0	0	0	0.002
Balaenoptera acutorostrata	0	0	0	0	0	0	0.009	0	0	0.001
Unidentified delphinid	0	0.030	0.010	0.009	0.025	0.043	0.035	0.010	0	0.021
Unidentified mysticetes	0	0.004	0.005	0.005	0.004	0.004	0	0	0.005	0.003
Unidentified cetacean	0	0.004	0	0	0	0.004	0	0	0	0.001
TOTAL	**0.234**	**0.371**	**0.376**	**0.387**	**0.366**	**0.424**	**0.347**	**0.265**	**0.414**	**0.363**

Table 14. Number of sightings per year and species for the 30 Observation Points a) in total, and b) per hour of effort.

There was a total of 83 sightings of harbour porpoises with a total duration of 13.33 h. Faro Corrubedo (OP number 19) was the OP with most records, and most of the sightings were in SA 3 and 4 (Fig. 26, 276 c). No porpoise sightings were recorded at 11 stations, including all five stations in SA.5 and those in the Ría of Vigo (OP 25, 26, 27). These differences between subareas are highly significant ($\chi 2 = 26.97$, d.f.= 5, $p<0.001$).

The year with most sightings of porpoises was 2011; 2007 was the year with fewest records except for the three months of survey in 2003 when no porpoises were detected (Fig. 27 a). Through the year, there are differences between months in the number of porpoise sightings. The month with fewest sightings records is November, although February, June and August all have only one more record (Fig. 27 b); July was the month in which most porpoises were seen.

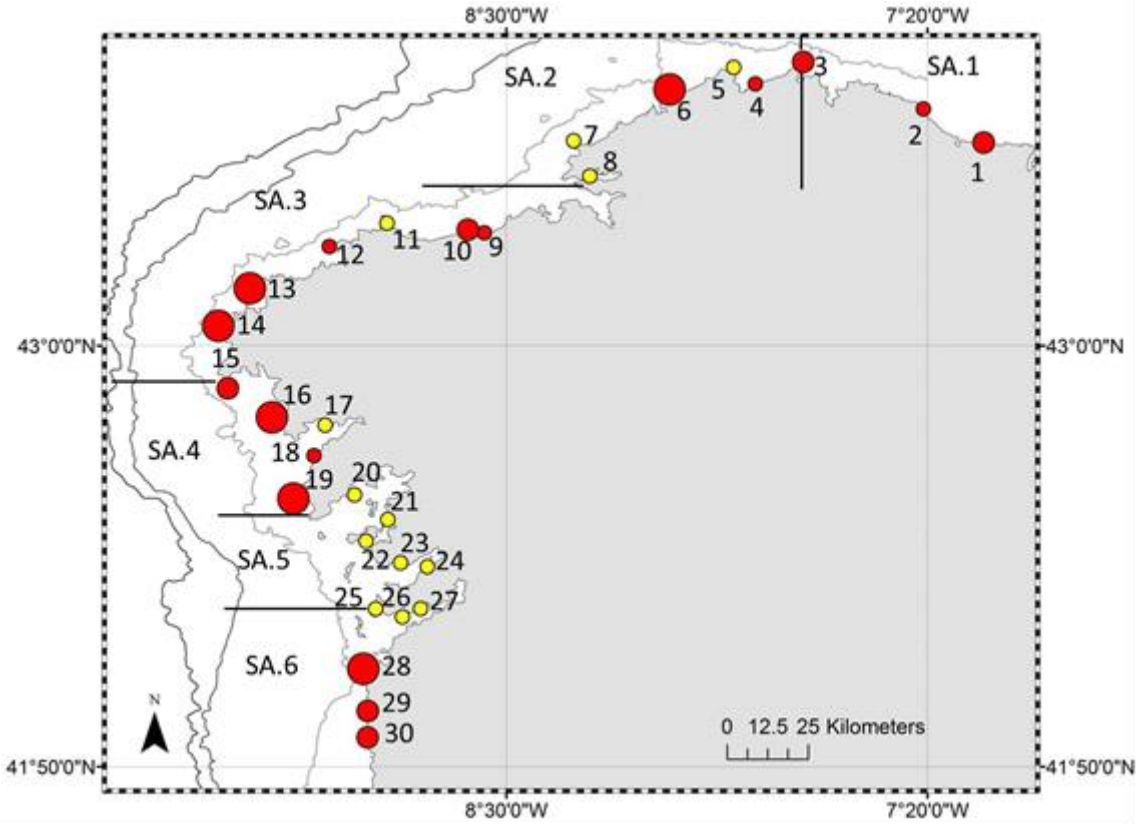


Figure 26. Sightings of harbour porpoise from data collected at 30 observation points along the coast from 2003 – 2011. Red dots are Observation Points at which sightings were carried out. The size of the dot depends on the number of sightings. Depth lines of 100, 200 and 500 m are also represented.

Although the difference between years was found to be significant ($\chi2$= 19.07, d.f. = 9, $p<0.05$), the difference between months was not significant ($\chi2$=13.45, d.f.=12, $P>0.05$). If the differences (between subareas) in the number of sightings are examined through the years (Fig. 27 d) or months (Fig. 27 e) along the coast, no clear patterns are detected. There was no significant interaction between year and SA effects ($\chi2$= 3.14, d.f.= 11, $P>0.05$), but there was a season and SA interaction ($\chi2$= 44.25, d.f.= 15, $p<0.005$). To analyse this interaction a GAM was carried out (Y ~ 1 + as.factor(SA) + s(Season, k=4, by = as.factor(SA)), Deviance explained 6.22%) and showed that there were differences in the distribution of the probability of detecting porpoises in four subareas (Fig. 28): in SA.2 and SA.3 there was a linear increase in the number of sightings since the beginning of the year, in contrast in SA.4 and SA.6, what was found was a decrease in the detection of porpoises since January until the end of the year. This could mean that porpoises move from the northern areas to the southern areas along the year.

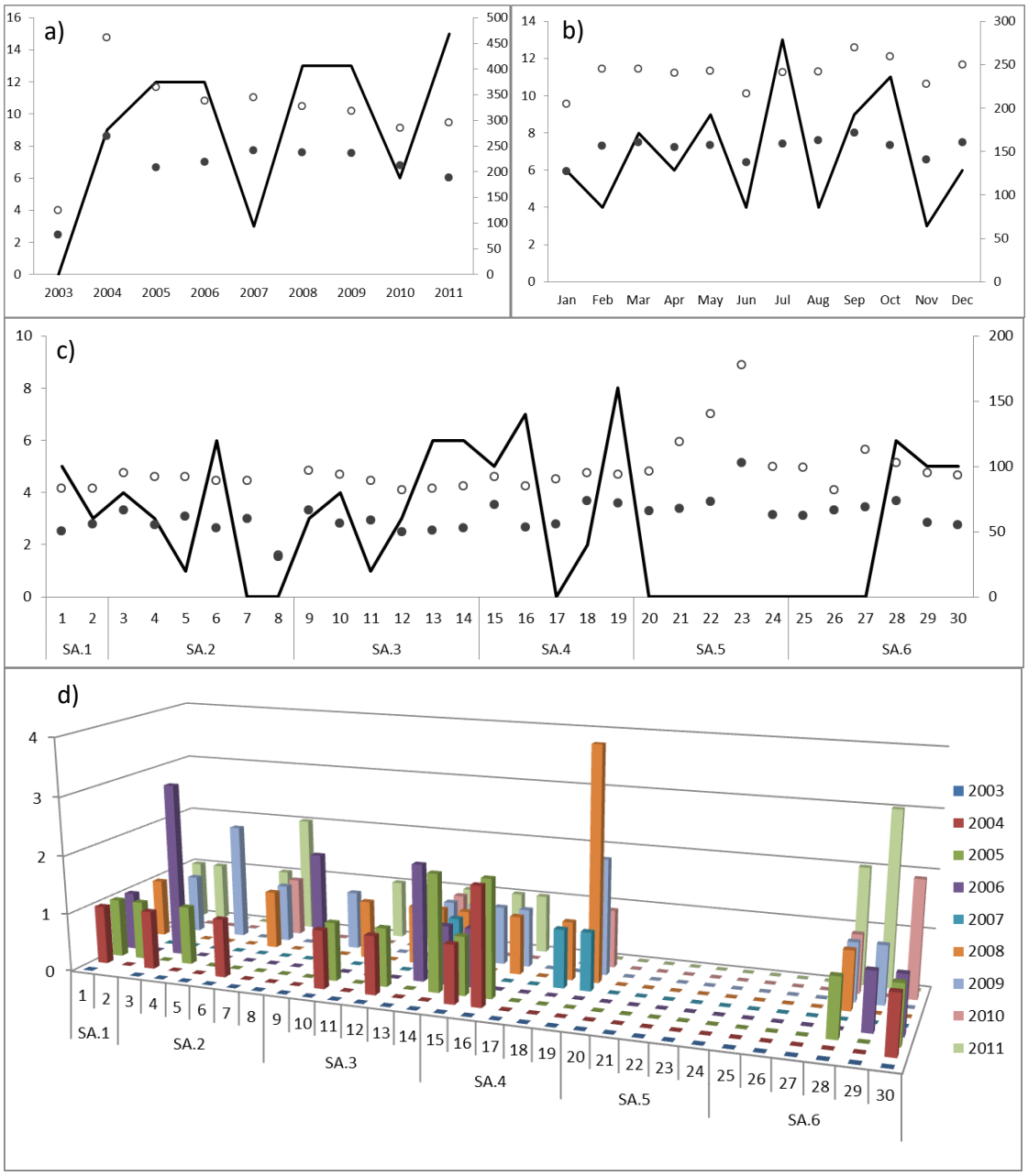


Figure 27. Mean numbers of sightings of harbour porpoises from coast surveys at 30 observation points, a) per year, b) per month, c) per observation point, d) per year and observation point, e) per month and observation point. In the graphs a), b), c) they are also shown the hours of observation (back dots) and number of observation periods (white dots) on the right axis.

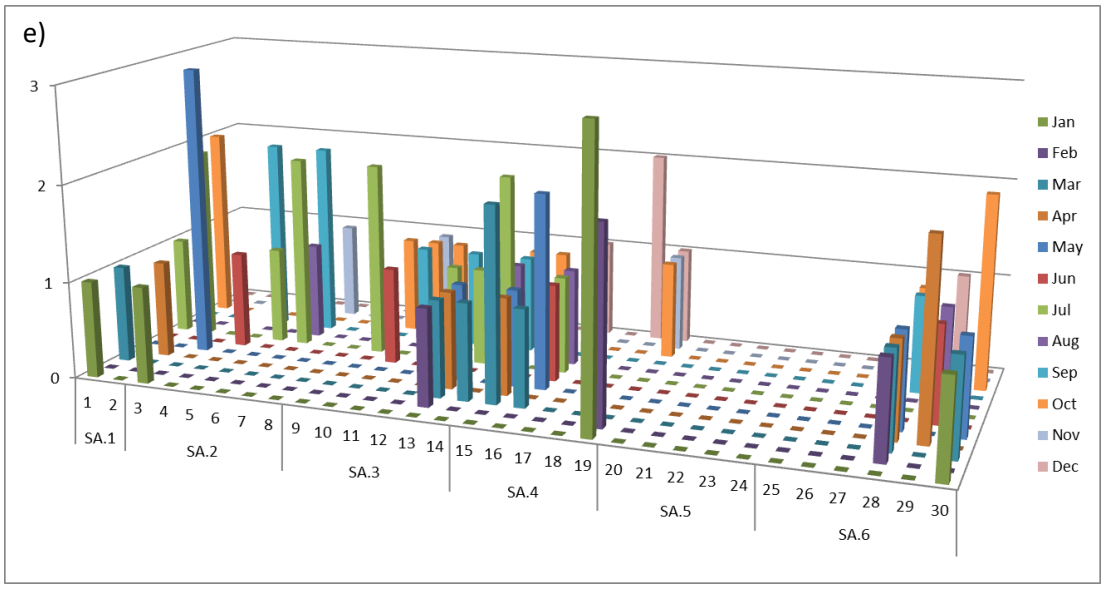


Figure 27. Continued.

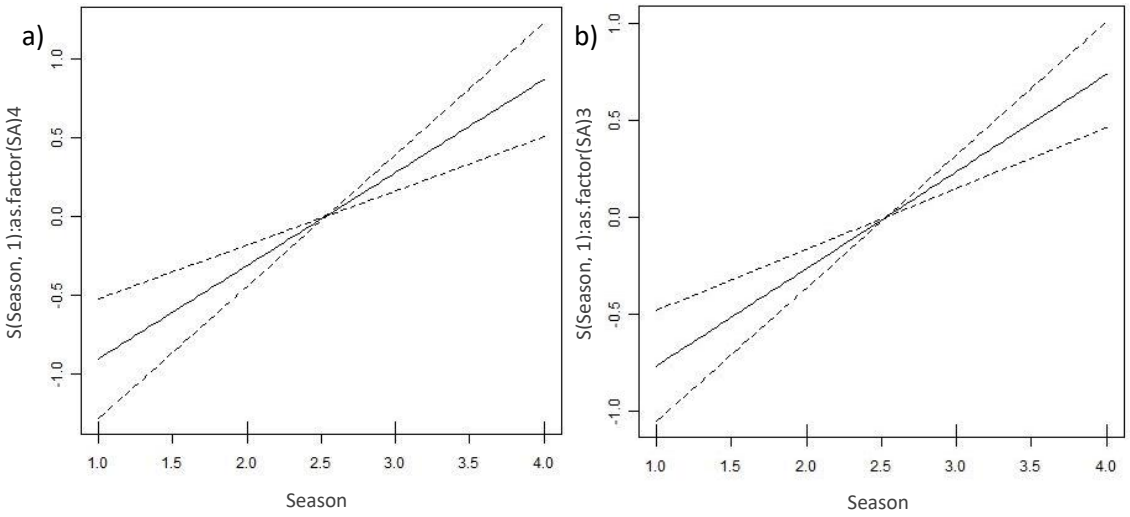


Figure 28. GAM showing the interaction between season and Sub-Area in the distribution of the probability of detecting porpoises. Significant subareas were: a) SA.2, b) SA.3, c) SA.4, d) SA.6.

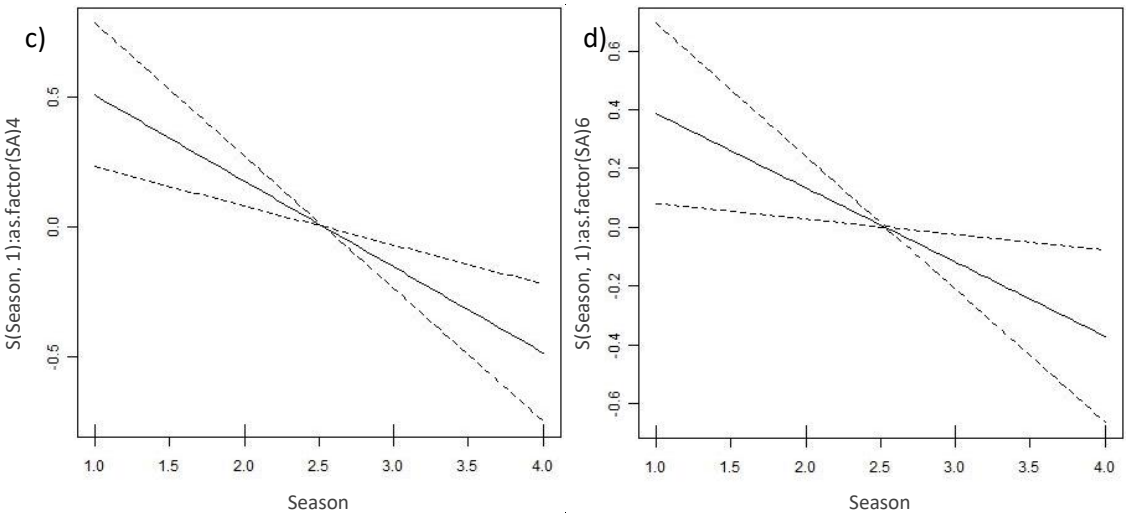


Figure 28. Continued.

The mean encounter rate for harbour porpoise was 0.044 sightings per hour; 2011 was the year with the highest encounter rate and 2007 was the year with the lowest encounter rate (Fig. 29 a). The months with most sightings were also the ones with highest encounter rates (Fig. 27, 29 b). In relation to both seasonal and year-to-year patterns, the highest encounter rates corresponded with highest number of sightings (Fig. 27 a, b, 25 a, b) 2005 and July respectively. Along the coast, the OP.16 (Punta Remedios, Lira) was the point with highest ER and OP.5 (C. Ortegal) and OP.11 (C. San Adrián) had the lowest values of ER (Fig. 29 c). Between sub-areas, SA.1 had the highest ER and SA.6 had the lowest ER (Fig. 29 c, 30).

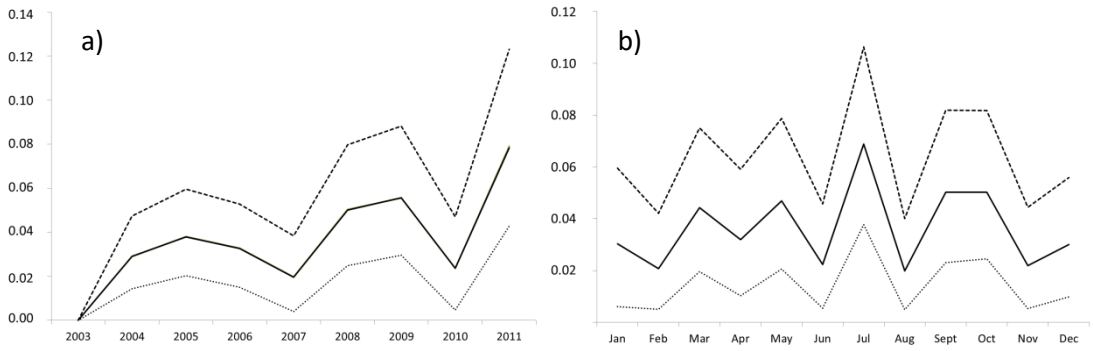


Figure 29. Variation of the average encounter rate for harbour porpoise a) per year, b) per month and c) per Observation Point. Dashed lines: upper 95% interval, black lines: overall, dots lines: lower 95% interval.

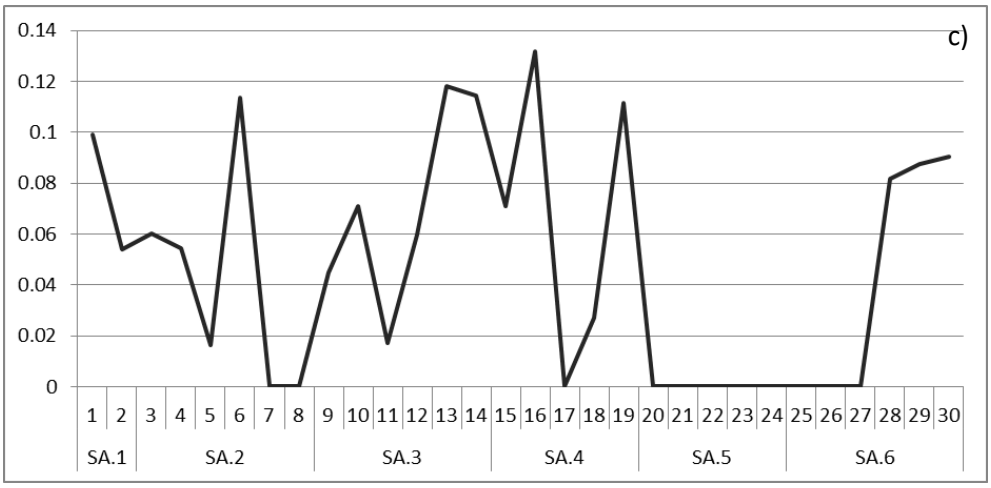


Figure 29. Continued

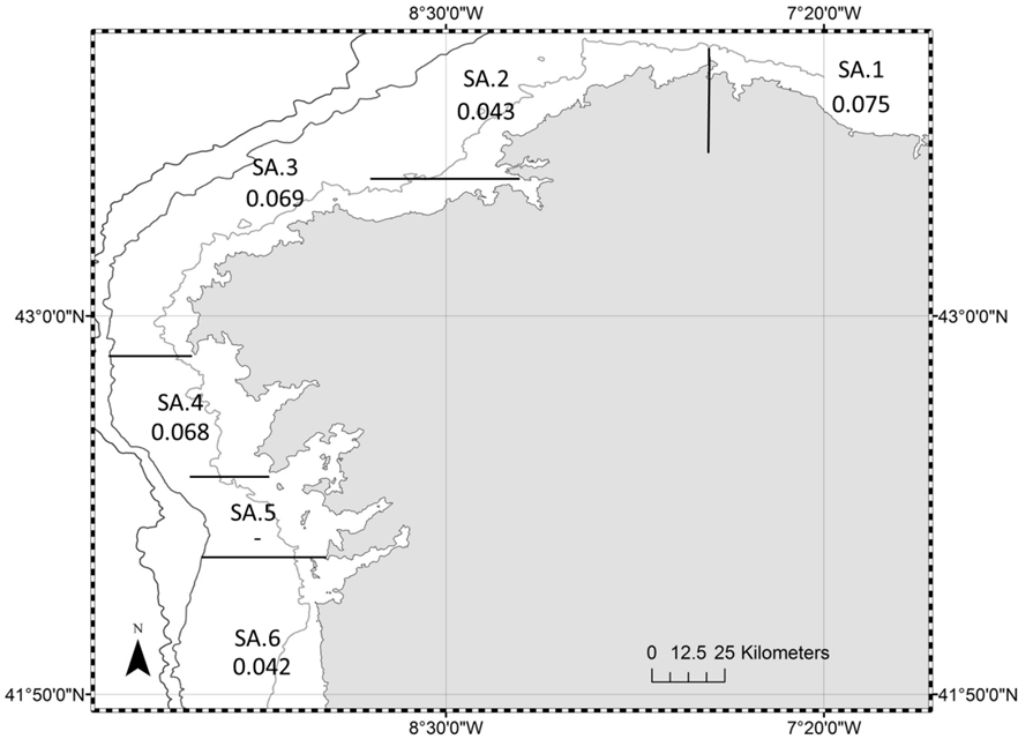


Figure 30. Encounter rate (ER) for harbour porpoise by Sub-Area expressed as number of sightings per hour.

Significant differences in mean group size were detected between years, months and areas (Table 15 a, b) ($\chi2=23.15$, d.f.=10, $p<0.05$; $\chi2=54.14$, d.f.=14, $p<0.005$; $\chi2=28.81$, d.f.=7, $p<0.001$; respectively). The highest average group sizes were found in 2009 (3.5 individuals), August (4.0 individuals), SA.1 (4.5 individuals) and at Stations 5 and 11 (5 individuals). In contrast, the smallest average group sizes were found in 2007 (1.3 individuals), December (1.5 individuals), SA. 6 (1.7 individuals) and at Observation Points 18 and 28 (1.5 individuals).

Only two sightings were inside the rías (Ría of Muros, Observation Point 18) and most of them were in waters of between 10 m and 50 m of depth (Fig. 31).

a)

2003	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**			
-	2.9	3.3	2.1	1.3	2.8	3.5	1.5	3.3			
Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
2.0	1.8	2.6	3.2	2.0	2.5	3.5	4.0	2.8	2.8	6.7	1.5

b)

SA.1		**SA.2**						**SA.3**						**SA.4**				
4.5		3.7						3.1						2.2				
1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
3.8	5.7	1.8	4.0	5.0	4.7	-	-	2.7	4.3	5.0	2.0	3.3	2.7	3.4	1.9	-	1.5	2.0

SA.5					**SA.6**					
-					1.7					
20	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
-	-	-	-	-	-	-	-	1.5	2.0	1.6

Table 15. Variation of the mean group size for harbour porpoise for a) year and month and b) Sub-Area and Observation Point.

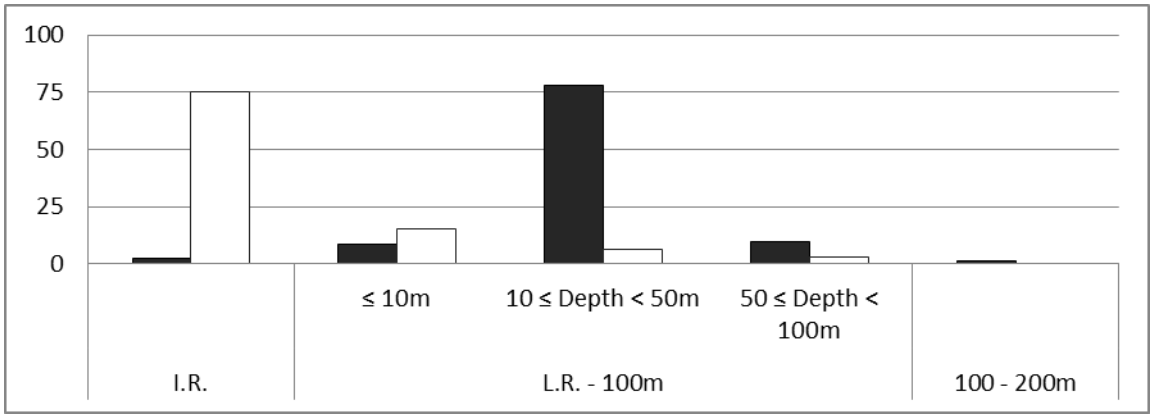


Figure 31. Distribution of the number of sightings of harbour porpoises (black) and bottlenose dolphins (white) sightings depending on the depth classes. L.R. limit of Rías, I.R. Inside Rías.

Comparing the sightings of harbour porpoises with the most common species along the Galicia coast waters, the bottlenose dolphin, the latter was seen mostly inside the rías, where few sightings of porpoises were recorded (Fig. 31, 32, 33 c). There were five stations at which only porpoises were seen and six at which there were no sightings of either bottlenose dolphins or harbour porpoises. The number of sightings of bottlenose dolphins per year was more variable

than for porpoises, and bottlenose dolphin sightings declined over the study period ($\chi 2=1046.97$, d.f.= 9, $p<0.001$). Porpoise presence was more constant through the years (Fig. 33 a).

In contrast, neither species showed clear monthly patterns. There was no obvious relationship between monthly sightings of the two species (Fig. 33 b). To study if there were differences in the distribution of bottlenose dolphin sightings between season and SA, a GAM was fitted (Y ~ 1 + as.factor(SA) + s(Season, k=4, by = as.factor(SA)), Deviance explained 11.6%) showing that there was an effect of season in four subareas (Fig. 34): in SA.2 there was a decrease in bottlenose dolphin sightings in summer and autumn, in SA.3 there was a peak in summer, in SA.5 which was no significant for porpoises there was an decrease along the year and, finally, in SA.6 in contrast to last subarea there was an increase since the beginning of the year, this result found in SA.6 was the opposite of what was found for porpoises. Considering the encounter rate (ER) for both species (harbour porpoise, bottlenose dolphin), higher values were found for bottlenose dolphins (Fig. 35 a-c). Some differences were detected in the distribution of sightings: for dolphins there was less variation between years. When ER for both species at each OP was studied, differences between areas with highest values of ER for each species were clearer. For bottlenose dolphins, areas with highest ER were in S.A.2 and 3, while S.A.4 and 5, which correspond to the rías, were also important for the presence of this species. For harbour porpoises, in contrast, highest values of ER were found in North Galicia (S.A.1 and 2, and in S.A.3 and 6), where presence of bottlenose dolphins was less frequent (lower ER). The highest ER was found for bottlenose dolphins in S.A.5 and 6, at Udra Cape and Ons Island.

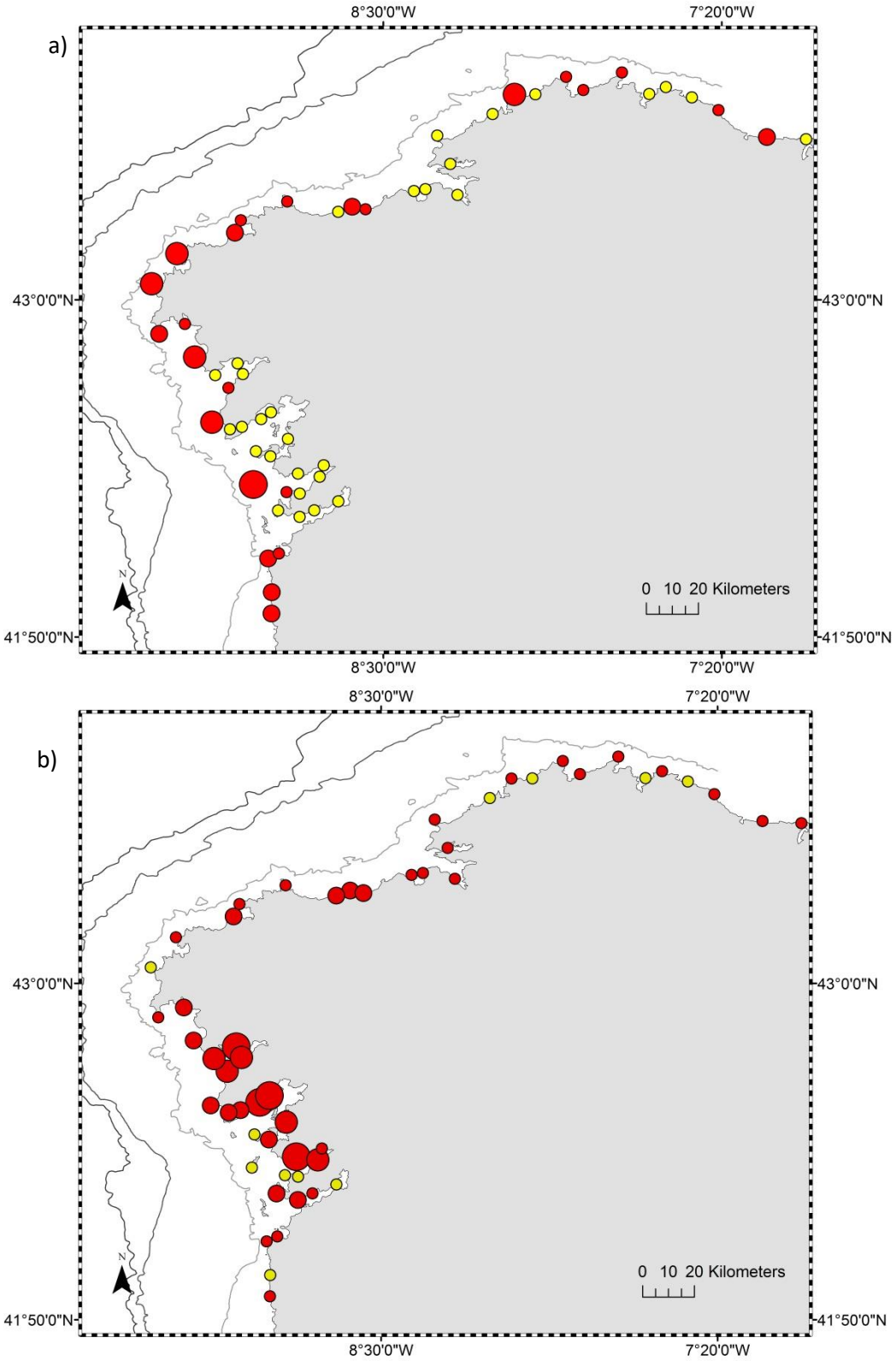


Figure 32. Sightings corrected by effort of a) harbour porpoise and b) bottlenose dolphin, from all data collected from 2003 to 2011. The size of the dot depends on the number of sightings. Depth lines of 100, 200 and 500 m are represented.

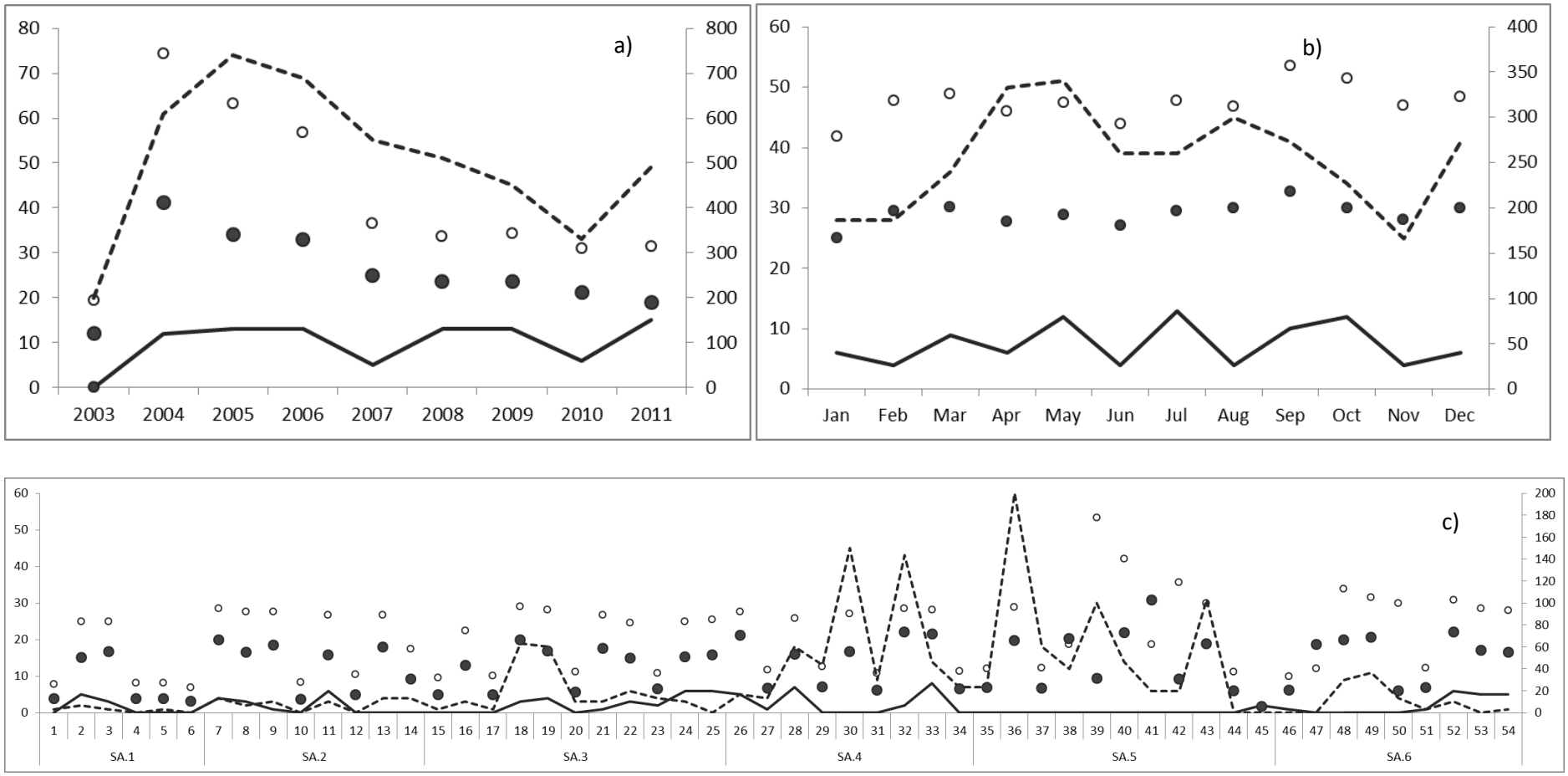


Figure 33. Comparison of sightings of harbour porpoises (black line) and bottlenose dolphins (whitedashed line) on the left axis, hours of observation (closed circles) and number of observation periods (open circles) on the right axis per a) year, b) month, and c) observation point.

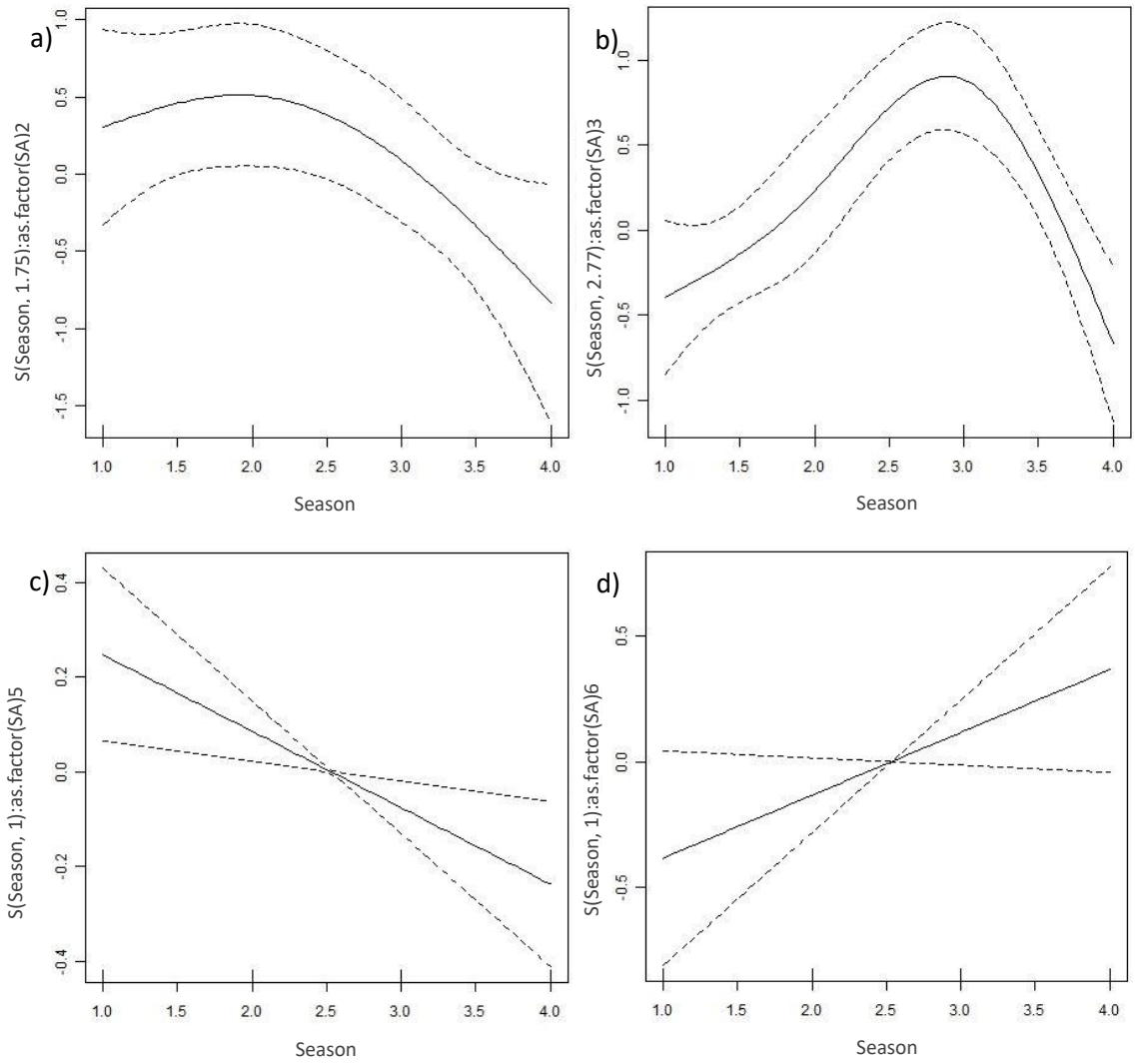


Figure 34. GAM showing the interaction between season and Sub-Area in the distribution of the probability of detecting bottlenose dolphins. Significant subareas were: a) SA.2, b) SA.3, c) SA.5, d) SA.6.

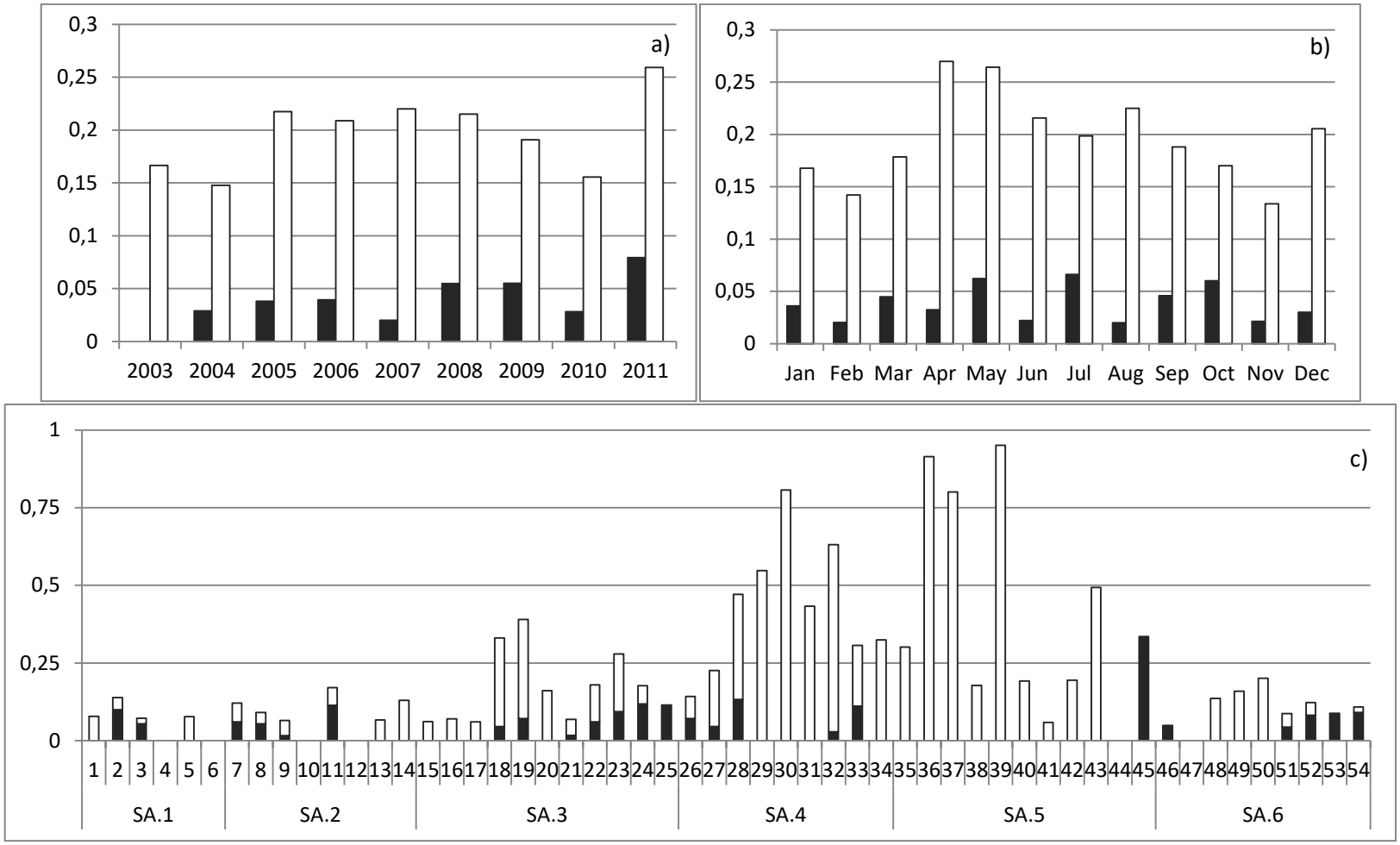


Figure 35. Comparison of average encounter rate (ER) of harbour porpoises (black) and bottlenose dolphins (white) per a) year, b) month, and c) observation point.

Models and selection criteria.

When modelling the effect of the environmental covariates on the observers, a total of 33 models were fitted (Annex XI an XII). The final model was the one with lowest AIC value and highest percentage of deviance explained. This model, where Y = porpoise presence, includes 5 explanatory variables:

Y ~ 1 + s(Obs_min, k=3) + s(Area_km^2, k=3) + s(Beaufort, k =3) + s(Sight_TTR, k=3) + s(Douglas, k=3) (AIC 743.06, Deviation Explained 11.6%).

The model shows a positive relationship between sightings of harbour porpoises and the duration of the observation period, for periods of up to approximately 100 minutes (edf=1.85, P < 0.001, Fig. 36 a). A similar relationship was found for the km^2 of area covered, for areas of up to around 30 km^2 (edf=1.78, P < 0.001, Fig. 36 b). The model also showed a linear decrease in sightings of harbour porpoises as the Beaufort value increases (edf=1, P < 0.001, Fig. 36 c), and bottlenose dolphins were detected (edf=1, P < 0.001, Fig. 36 d). Porpoises were most frequently seen when Douglas values were in the range 2 to 3 (edf=1.72, P < 0.001, Fig. 36 e).

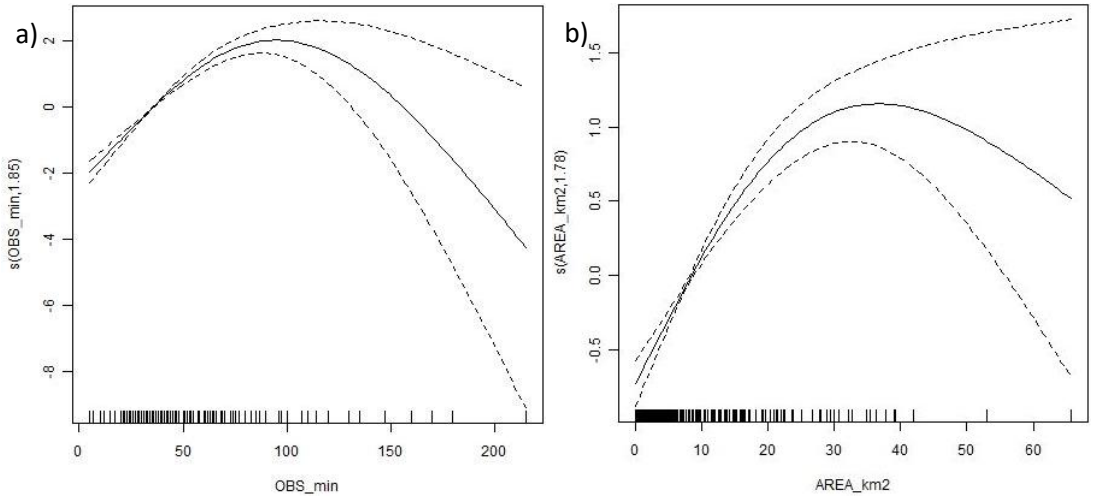


Figure 36. GAM results: smoothers showing partial effects of environment on the observers. Covariates: a) duration of the observation (min), b) area covered at the survey (km^2), c) Beaufort, d) sighting of bottlenose dolphins, e) Douglas.

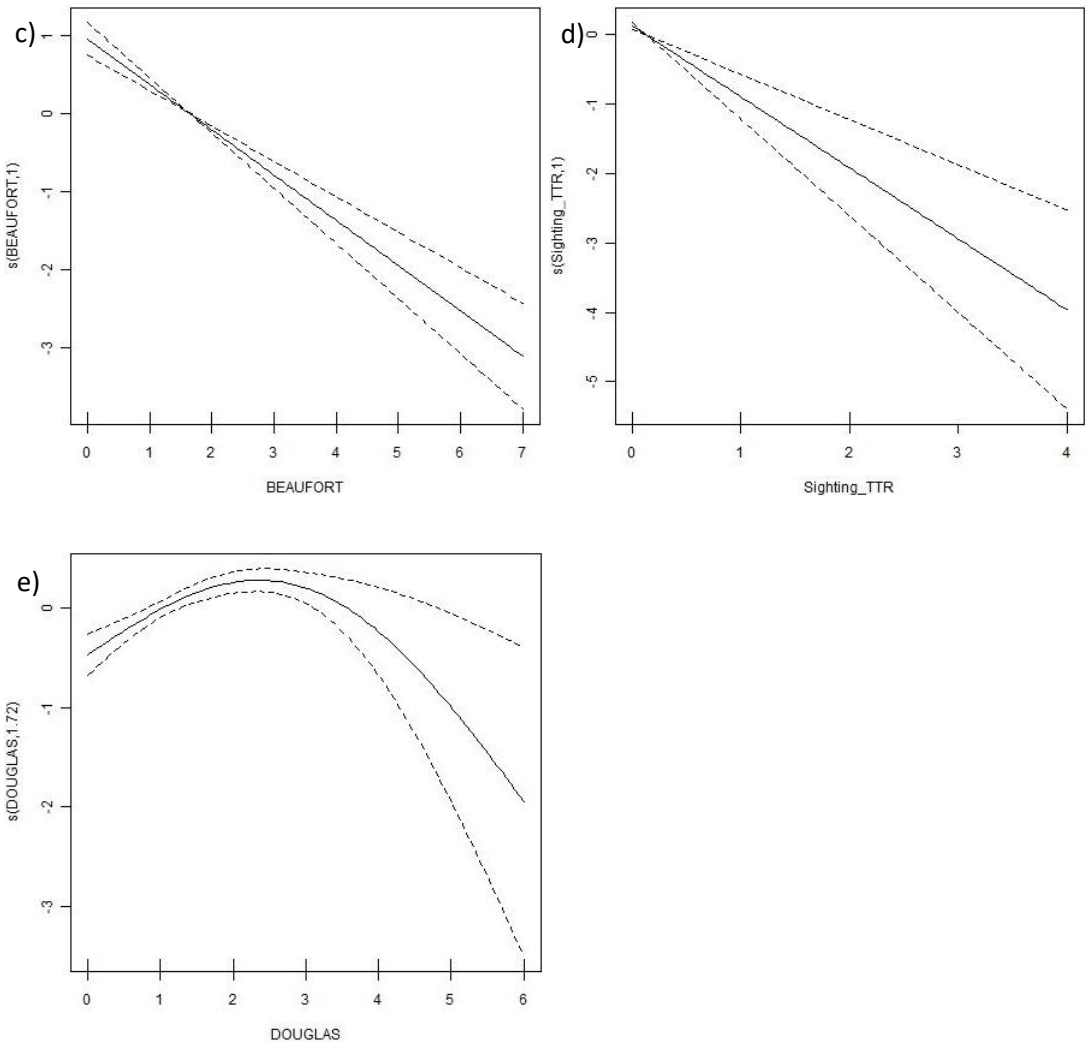


Figure 36. Continued.

Then GAM models were fitted with the variables affecting observation plus spatio-temporal covariates (i.e. year, month, time of day, PC). A total of 17 models were fitted (where Y = porpoise presence; Annex XIII and XIV), and a final best model with all the covariates significant and with the lower AIC was selected:

Y ~ 1 + s(OBS_min, k=3) + s(AREA_km^2, k=3) + s(BEAUFORT, k=3) + s(Sighting_TTR, k=3) + s(YEAR, k=4) + s(START_OBS, k=4) + s(OP), 709.11AIC, 17.2% of deviance explained.

The partial effects of these covariates are shown in Fig. 37. The covariate Douglas, which was statistically significant in the previous model, become non-significant and it was dropped out. The other covariates kept from the model fitted for the effect of the environmental co-variables on the observers remained significant and with the same effects, only the effective degrees of freedom changed for AREA_km^2 (edf=1.82, P < 0.001, Fig. 37 b). There was a linear

increase of sighting rates as the observation period increases (OBS_min; edf=1.85; P < 0.001, Fig. 37 a) from the first year of study to the last one (edf=1, P< 0.0001; Fig. 37 e); there was also a linear increase in the probability of detecting porpoises with the time of the day at which observations took place (START_OBS; edf=1, P < 0.0001; Fig. 37 f). There was a negative linear relationship between sightings of harbour porpoises and the position of the station along the coast (edf=1, P < 0.0001, Fig. 37 g), the probability of detecting porpoises being higher at the OP in the North-east than at those in South Galicia.

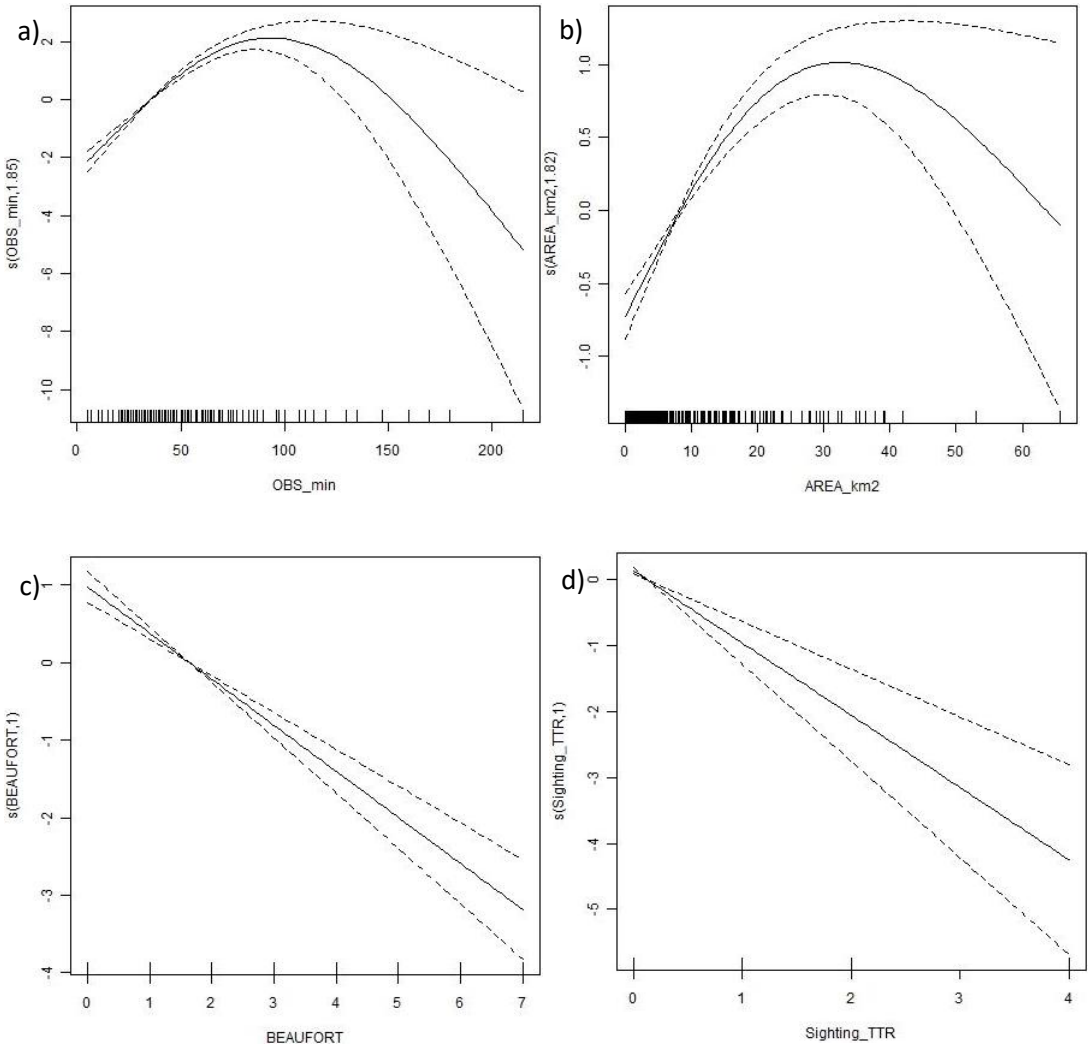


Figure 37. GAM results: showing partial effects of time and space covariates: a) duration of the observation (min), b) area covered at the survey (km^2), c) Beaufort. Also illustrated are smoothers showing partial effects of habitat covariates: d) sighting of bottlenose dolphins, e) year, f) the time of the day at which observations begun, and g) observation point.

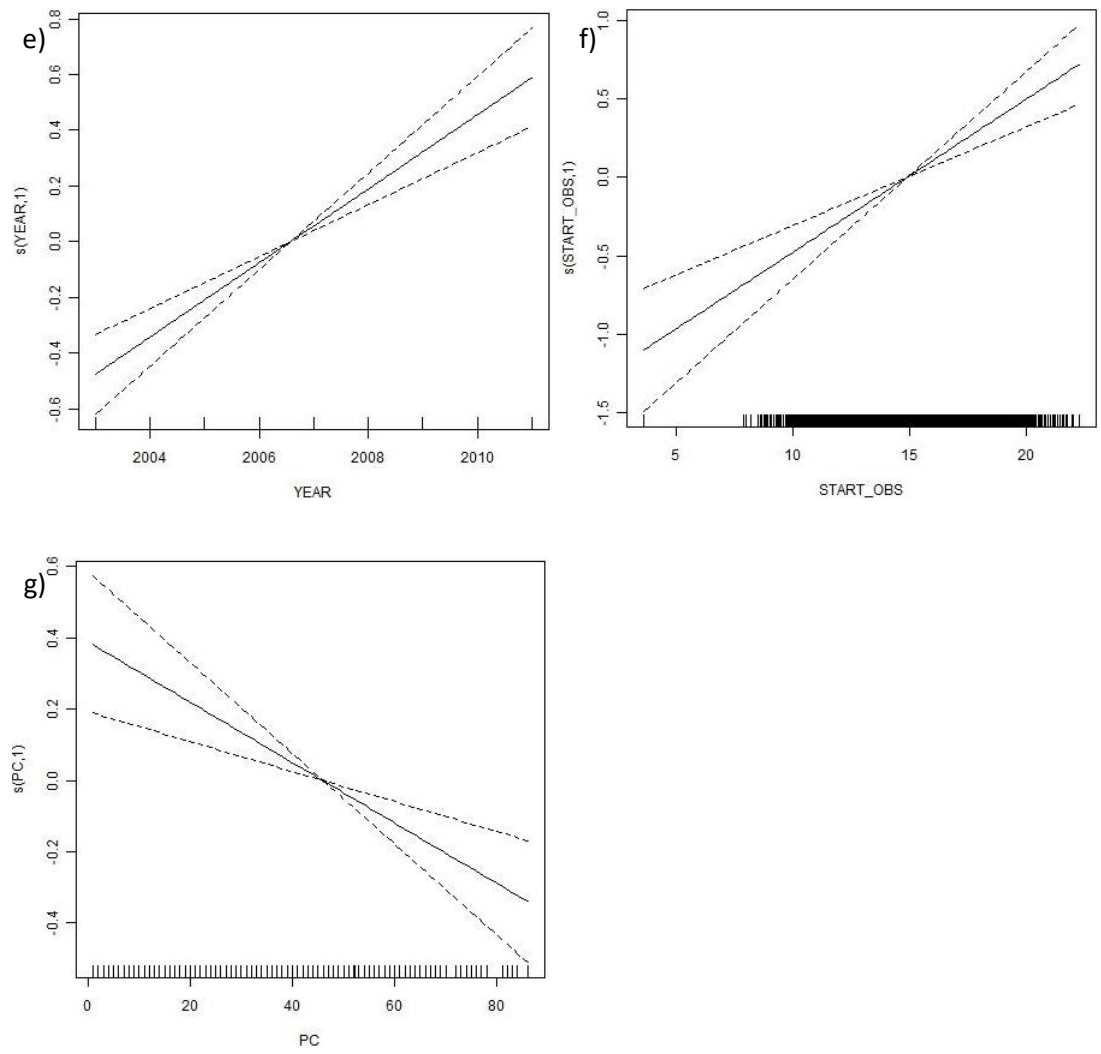


Figure 37. Continued.

Finally, GAM models were fitted with the variables affecting observations plus habitat covariates. As the number of covariates was high, to streamline the model selection process, when a variable was not statistically significant it was dropped out. Two of the covariates that were statistically significant in the previous model, Douglas and sightings of bottlenose dolphins, became non-significant and were dropped out. Of a total of 274 models fitted (where Y = porpoise presence; Annex XV and XVI), 15 models were found to have very similar AIC, but the model with all the covariates significant and with the lowest AIC was:

Y ~ 1 + s(OBS_min, k=3) + s(AREA_km^2, k=3) + s(BEAUFORT, k=3)+ s(W_Northing, k=4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(D_200m, k=4), 541.09 AIC, 22.7% of deviance explained.

The partial effects of these covariates are shown in Fig. 38. For the three covariates kept from the model fitted for the effect of the environmental co-variables on the observers, the effect and statistical significance were the same, but the effective degrees of freedom changed for OBS_min (edf=1.9, P < 0.001, Fig. 38 a) and AREA_km^2 (edf=1.88, P < 0.001, Fig. 38 b). For the habitat covariates, all variables have a linear effect except W_northing and DEP_STD. There were more sightings when the wind came from the East (edf=1.95, P < 0.05, Fig. 38 d) and for areas with more variability in depths (edf=2.88, P < 0.05, Fig. 38 g).There were positive linear increases of sightings with increases in the slope (edf=1, P < 0.05, Fig. 38 e) and in ZEU (edf=1, P < 0.1, Fig. 38 f), while the effects of both POP_STD and DIST_200m were negative and linear, with a decrease in the probability of sighting porpoises with an increase of the standard deviation of the density of the human population in the area (edf=1, P < 0.01, Fig. 38 h) and an increase in the distance from coast to the isobath of 200 m depth (edf=1, P < 0.01, Fig. 38 i), thus when the platform is wider.

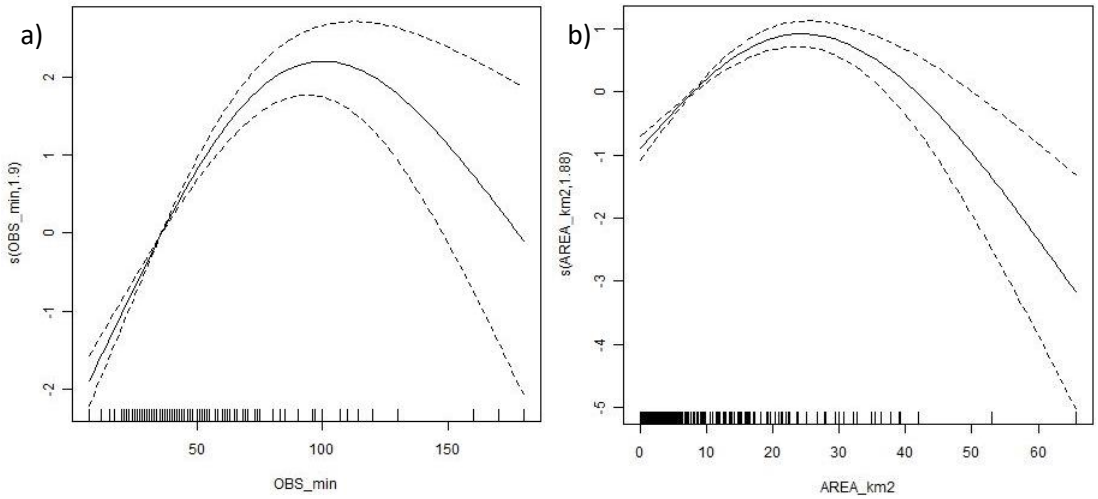


Figure 38. GAM results: showing partial effects of environment on the observers: covariates: a) duration of the observation (min), b) area covered at the survey (km^2), c) Beaufort. And smoothers showing partial effects of habitat covariates: d) wind aspect northing, e) mean value of the sea slope, f) mean values of the euphotic depth (m), g) standard deviation of the depth (m), h) standard deviation of the human population (individuals per km^2), i) distance from coast to the 200 m isobath (decimal degrees).

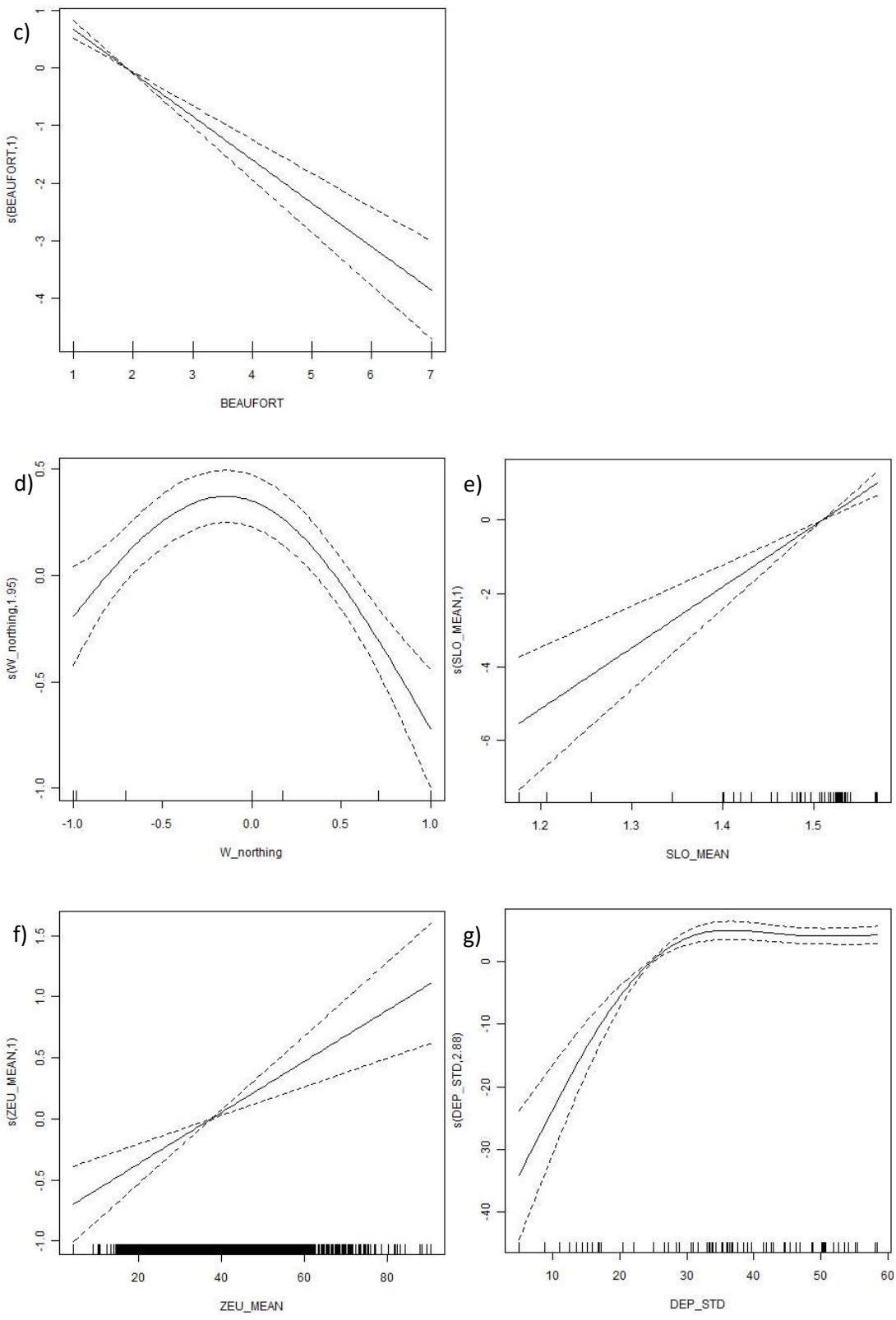


Figure 38. Continued.

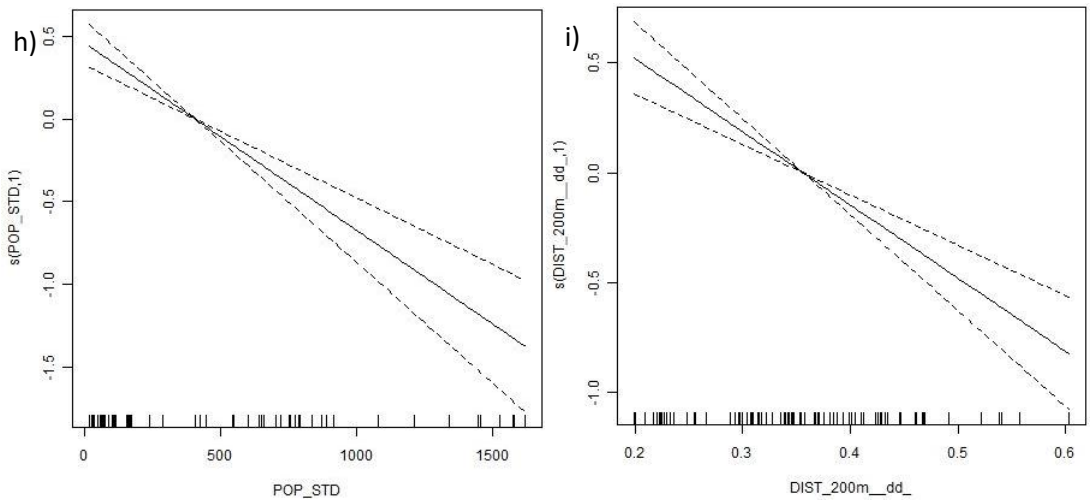


Figure 38. Continued.

Discussion

For the monitoring of cetaceans in Galician waters, land-based surveys were carried out from a series of observation points along the coast to cover the study area as evenly as possible. This method has the advantages of being low cost, has the possibility of surveys all year around and it is effective to study temporal and spatial trends and provide important information on species presence and relative abundance in coastal waters (Evans and Hammond 2004). Moreover, land-based surveys prevent one of the main factors leading to the over- or underestimation of cetacean abundance since the cetaceans are not influenced by the presence of survey boats by avoiding or being attracted to them (e.g. Palka and Hammond 2001, Williams et al 2002 a, b, Cañadas and Hammond 2008, Scheidat et al 2004, Lusseau 2006, Christiansen et al 2010). On the other hand, there are also some obvious disadvantages such as the limitation of studying only coastal species (Carretta et al 2001, Cañadas et al 2003, Santora 2012), and the restriction of monitoring only those areas visible from the coast.

Various factors can have some influence on the detection of cetaceans by observers during land-based (and/or boat-based surveys) and should be taken into account. This is especially important for harbour porpoises, which are small in size, have cryptic surfacing behaviour (it is relatively rare to see more than the dorsal fin and a part of the back), doing long dives between breathing sequences, spending little time at the water's surface, and they are often solitary (Westgate et al 1995, Read 1999, Heide-Jørgensen 2013). Thus harbour porpoises are difficult to detect. If those variables that can affect their detection by observers are not considered, together with porpoise behaviour, there could be an underestimation of the population or even an incorrect interpretation of lack of sightings as absence in an area.

The harbour porpoise is a species that in general forms small groups consisting of a few individuals (Read 1999). In Galicia, porpoises were found to occur as solitary individuals or in groups of up to 8 individuals, although most of the sightings were of solitary individuals or pairs. However large aggregations of tens to hundreds of individuals have been recorded in the Western North Atlantic (Hoek 1992). In the present study there were differences in the size of the groups between different years, months and subareas, but there was no clear trend in those variations.

In the present study five variables were found to have some influence on the observers in relation to the detection of porpoises. As mentioned above, porpoises are difficult to detect, and therefore, the more time that the observers have available to search for porpoises at the

station, the higher the probability of detecting them if they are present in the area. Because the observers can get tired, there also should be a maximum duration of the observation period to avoid a decrease in the efficiency of the search, which in the current study begins approximately at 100 minutes. Something similar happens with the area available for survey (i.e. the field of view): in larger areas the probability of porpoise detection increases but also if it is too big the observers will probably not scan all the area with the same effectiveness and detection probability would be expected to reach an asymptote.

In addition, many authors have identified sea state (e.g. expressed as Beaufort and/or Douglas), as an important factor for the detection of porpoises (Palka 1996, Evans and Hammond 2004, Weir et al 2007, Tynan et al 2005, Marubini et al 2009, Embling et al 2010, Pierce et al 2010, Booth et al 2013, Dolman et al 2013, de Boer et al 2014, Chapter III). The present study also found that sea state had an important influence on the (apparent) presence of porpoises. However, interestingly, whereas Beaufort has a clear negative linear relationship with detection of porpoises, Douglas has a positive effect until values of 2. In addition, when analysing the spatial and temporal trends or effects of environmental conditions, the best models fitted all excluded the Douglas variable. This might indicate that Beaufort has a more significant impact on the detection of porpoises and/or that the effect of the Douglas value is masked by effects of other environmental covariates.

Finally, the presence of bottlenose dolphins was also found to be important, being negatively correlated with detection of porpoises. This is another species common in Galician coastal waters (López 2003, Lopez et al 2004, Pierce et al 2010, Spyrakos et al 2011) and may have an influence on the distribution of porpoises due to the possible avoidance by porpoises of competition and/or attacks (López and Rodríguez 1995, Alonso et al 2000, Mendez-Fernández et al 2013). In addition, the presence of dolphins might distract observers from seeing porpoises. However, it is important to note that an apparently negative relationship could arise simply due to the two species having different habitat preferences. Once the conditions that affect the detection of harbour porpoises were taken into account, a temporal trend was found during the study period, with an increase in the number of sightings over the years. A previous analysis of part of the current dataset, using data up to 2007 (Pierce et al 2010), did not find such a trend, although more porpoises were seen in 2004 than 2003. However, the longer time series available for the present analysis gives greater statistical power to detect interannual trends.

In addition, the interannual trend found here is different to results of a contemporaneous boat-based survey study (Chapter III), which found that 2005 was the year with most porpoise sightings and in which there were no detections in 2006. This could be due to the area surveyed, as boat-based surveys were focused on the South coast of Galicia, and porpoises could have left those areas and moved to other ones (moving North to northern Galicia or South to Portugal). In addition such differences could arise if porpoises spent more time close to the coast in some years. In principle this could be related to prey distribution and abundance, and thus linked to year to year variation in the strength of upwelling. Although it seems that there is no relationship between years and high upwelling index. It could be related with the time needed to transfer the nutrients through the food web, as was found for *Octopus vulgaris* planktonic larvae (Otero et al 2009), with a significant increase in larval abundance and biomass with the upwelling relaxation. However, the time series is presently too short to investigate this.

The increase of number of sightings during land-based surveys could mean that the population is growing. It is known that Galician porpoise population sex ratio is close to 1:1 (Read et al 2012, Chapter IV), if it is assumed that half of the females are sexually mature (Read et al 2012), and that there is an annual mortality rate of 18% (Read et al 2012), the population could grow a maximum of 7% (25%-18%), which is lower than the apparent increase seen in the present study (and indeed already assumes a pregnancy rate of 1.0 whereas most estimates for European populations are rather lower). Another reason that could explain the rise in sightings detected could be the movement of individuals from other areas such as Asturias or Portugal, or even from distant areas to areas closer to the coast in Galicia, but there are insufficient data from there at present to evaluate this possibility.

In addition, a temporal trend during the day was found, which showed an increase in the number of sightings later in the day, as indeed was found before by Pierce et al (2010). The reason why more sightings were recorded later in the day could be due to boat traffic. It is known that porpoises tend to avoid boats (Culik 2004, personal observation). Thus, when maritime traffic decreases at that time of the day, the animals could begin to use the areas closer to the coast.

There was also a spatial trend in the number of sightings with more detections in Lugo and A Coruña (Northern stations), which is again broadly consistent with previous analyses (Pierce et al 2010), which found that the sightings were more frequent around Punta Roncadoira (between observation points 2 and 3 in this work), and Cabo Vilán (observation point 13). In

contrast, the peak found in that study in A Guardia (observation point 30, adjacent to the border with Portugal) was not detected here. This decrease in the number of sightings in the south of the study area could mean that porpoises are changing their distribution and are moving to northern areas of Galicia or indeed south to Portugal. It seems that Galician porpoises prefer areas with fewer and smaller rías, and avoid industrialized areas, such as the Rías of A Coruña, Pontevedra and Vigo. Also, one of the most important factors affecting porpoise presence was the presence of bottlenose dolphins, and they were detected mostly in those three rías.

A striking feature of the oceanography of the Galician coast is the occurrence of upwelling (e.g. Fraga 1981, Prego and Varela 1998, Figueirias et al 2002). The interaction of a meridional density gradient with the slope and wind forcing generates a poleward flow in the western boundary region (Gil 2003) below the surface (Huthnance et al 2002, Mason et al 2006) that often extends to the surface during winter. Slope currents are stronger and more persistent than shelf currents and have an onslope tendency in mid depths (Pingree and Le Cann 1989). In Galicia, this current is referred to as the Iberian Poleward Current (IPC) (Peliz et al 2003). It was confirmed that the adjustment of a meridional density gradient to a meridional oriented slope is likely to be the central mechanism in the generation of IPC (Peliz et al 2003), that together with the topography creates surface features such as eddies along the slope. Eddies have been found to be important sources of food for fish, marine mammals, cephalopods and birds (Dower and Perry 2001).

Upwelling conditions have been described as one of the most important variables influencing the presence of porpoises in California (Tynan et al 2005), Eastern North Sea (Skov and Thomsen 2008), and the German Bight (Gilles et al 2011). The present study suggests that in Galicia such conditions also have an important influence on the presence of porpoises, which reflects the presence of high productivity conditions. Porpoise detections increased when there were Eastern winds. Although upwelling is correlated with wind from North, along the Galician coast, those Eastern winds can also create conditions of upwelling in this area, increasing the productivity of the area.

The depth of the eutrophic zone (ZEU) was significant in the models fitted. This zone is the depth range where the Photosynthetically Active Radiation (PAR) is sufficient to support photosynthesis (Kirk 2011). Thus, the highest values of ZEU indicate areas of high productivity (Haande et al 2011, Jin et al 2011, Khanna et al 2009).

Upwelling and primary productivity are related to higher trophic levels through the food chain. Highly productive areas of upwelling or eddies may be good for the development and aggregation of the most important prey of harbour porpoises in Galicia such as blue whiting, *Trisopterus* spp, silvery pout (*Gadiculus argenteus*) and *Trachurus* sp. (Pierce et al 2010, Read et al 2012) that can be found on the continental slope (blue whiting) and in shelf waters (the other species). Consumption of blue whiting implies foraging in slope waters. Porpoise distribution is likely to reflect foraging opportunities, but if the trends in distribution of blue whiting (ICES 2012) are compared with the ones of the distribution of sightings of porpoises, years with highest abundance of blue whiting are not related to years with lowest sightings, which would be expected if porpoises move to deeper water. By remaining close to food resources, porpoises may be able to more easily meet the energetic demands of maintenance, growth and reproduction. This is especially important in the case of mature females which have the additional costs of pregnancy and lactation that increase the energy requirements and may happen at the same time (Brodie 1995, Kastelein et al 1997, Read et al 1997, Read and Westgate 1997, Koopman 1998, Lockyer 2007, MacLeod et al 2007).

There are three more environmental variables which were found to have an influence on the presence of porpoises along the Galician coast. More porpoises were detected in waters where depth was more variable, sea bed slope was greater and the continental shelf was narrower. These will be areas where deep waters occur close to the coast, highlighting the importance of the areas where the shelf is narrower, which was also found by Pierce et al (2010), who argued that this could indicate that porpoises habitually occupy deep waters in Galicia. Since then, several studies confirmed this, showing that in this area porpoises are seen in waters with depths between 50 - 100 m, with several detections in even 100 - 200 m (Spyrakos et al 2010, Fernández et al 2013, Chapter III). Seabed slope was found to influence porpoise distribution in other areas (Embling et al 2010, Isojunno et al 2012, Booth et al 2013). FInally, although the importance of depth is clear, the relationships are different depending on the area. In Northwest Scotland porpoises were found to have preference for waters between 50 and 150 m depth (Marubini et al 2009), whereas in the Moray Firth Marine Protected Area they occurred in waters with a maximum between 10 to 35 m depth (although these were the sections of the study area with deepest water, Bailey and Thompson 2009). In Northern California, porpoise were most frequently seen over depths of 20 to 60 m and fewer porpoise than expected occurred at depths >60 m (Carretta et al 2001) while in the Bay of Fundy and Gulf of Maine, they were found most frequently in areas where depths range between 92 and

183 m (Read and Westgate 1997). It seems that preferred depths are a consequence of local conditions rather than being a consistent characteristic of porpoise habitat choice.

This variation could be due to the diet of porpoises. The principal prey varies between areas, with relatively few different species in each one, which live in distinct habitats. For example, whereas in Galicia porpoises' main prey are blue whiting, *Trisopterus* spp, silvery pout and *Trachurus* sp. (Pierce et al 2010, Read et al 2012), species mostly distributed in deep waters (Cohen et al 1990, Svetovidov 1986, Collete and Parin 1986, Smith-Vaniz 1986), in Scotland the main prey are sandeels (Ammodytidae) and whiting (Santos et al 2004), and in the Gulf of Maine it is herring (*Clupea harengus*) (Gannon et al 1998), which are found in waters of less than 200 m depth and generally are not present in the Galician waters (Whitehead 1985, Muus and Nielsen 1999, ICES 2012).

However it is not only "natural" conditions that seem to determine the distribution of porpoises. As mentioned before, porpoises were not detected inside the Rías, which are mostly located along the West and Southern coast of Galicia, and are more industrialized with more and bigger cities than other areas and where most bottlenose dolphin sightings occur. Although it is difficult to demonstrate cause and effect, since environmental differences, presence of bottlenose dolphins and anthropogenic impacts are potentially confounded, and areas with higher human population density were those with lower probabilities of detecting porpoises.

The best models fitted explained a relatively low proportion of the deviance, especially in the spatiotemporal model that explained 17.2% of the deviance (11.6% due to the variables that affect the observers and 5.6% due to spatiotemporal variables), whereas the environmental model explained 22.7% of the deviance (11.6% due to the variables that affect the observers and 11.1 % due to environmental variables). Such low values of deviance explained are not unusual in ecological studies (e.g. Cañadas and Hammond 2006, Embling et al 2010, de Boer et al 2014). However, it remains difficult to disentangle the separate effects of environmental conditions, other species and anthropogenic impacts. Therefore, it is important to carry out more studies including collection of additional data, especialy environmental aspects, such as coast type, tides, upwelling index, mesoscale oceanographic features, but also others such as maritime traffic, fisheries, contamination, water quality. Also, the implementation of the land-survey network with stations in the archipelagos of Cíes and Ons, and Sálvora Island, where harbour porpoises have been regularly detected, would help to establish if they are important areas for the species or not. This could not be done until now because the access to the islands

is difficult especially in winter and is controlled as they belong to the Parque Nacional Marítimo Terrestre das Illas Atlánticas de Galicia and have been defined as a Special Area of Conservation (SAC) including several species of amphibians, birds, fish, invertebrates, terrestrial mammals, reptiles and plants, but not marine mammals specifically. Although those areas are already protected, if the area is important for the species, new evidence should be taken into account and the connections with other areas used by porpoises should be guaranteed. Finally, the development of other studies such as acoustic studies, which could increase the hours of monitoring and provide useful supplementary data about the distribution of the species even at night, or the implementation of observation effort in the areas detected as especially used by porpoises, will complement the information about the use of those areas by them, giving additional knowledge about this species.

However, now the population of harbour porpoises in Galician waters is better known. When, where and in which environmental conditions they are present, are all important questions that need to be answered for their conservation. In Spain, although the Habitats Directive requires to the State Members the creation of SACs, no SAC has been established specifically for harbour porpoises. The results of this study provide essential information about this species in Galicia, which are important to keep in mind. For example, i) protected areas cannot be seasonal, because the species is present throughout the year, ii) one of the key areas in the Iberian peninsula, as is maybe also the case for the Gulf of Cadiz (Consejería de Medio Ambiente y Ordenación del Territorio 2015), is Galicia where there are four localities with particularly high occurrence of porpoises: Punta Candieira (Observation Point 6), Vilán and Touriñán Cape (Observation Points 13 and 14), Punta Remedios (Lira; Observation Point 16) and Faro de Corrubedo (Observation Point 19), iii) the main areas used by harbour porpoises and bottlenose dolphins are different, moreover, while a part of the bottlenose dolphin population was described as a resident population (Fernández et al 2011) porpoise population does not seem to behave in the same way, therefore the same SAC is not going to be useful for both species, only if it is big enough to cover those different areas.

Protected areas can help the recovery/maintenance of the target species as well as benefitting the whole ecosystem (Cañadas et al 2005, Sergio et al 2006, 2008, Notarbartolo-di-Sciara et al 2008). However, it has to be considered that with highly mobile species such as harbour porpoises, if detrimental impacts persist outside the boundaries of an SAC and, for example, impede porpoise movements between areas, increase their mortality, or reduce reproduction success, the conservation measures will finally not be effective.

In addition, cetaceans are defined as potential indicators for determining GES under the Marine Strategy Framework Directive (MSFD). Useful information can be obtained by the continuation of the land-based surveys. They will give the chance to detect variations in the ecosystems as the harbour porpoises are described as indicator species, through the analyses of their distribution and abundance. Moreover, in the future, it could help to evaluate the success of conservation strategies in maintaining the population in good condition or if more effort has to be invested in conservation measures.

CHAPTER V

Patterns and characteristics (length, sex, by-catch) of the strandings of harbour porpoise (*Phocoena phocoena*) in the North West Iberian Peninsula.

Ángela LLavona, Pablo Covelo, Juan I. Díaz, Jose A. Martínez-Cedeira, Marisa Ferreira, Jorge Santos, Helder Araújo, Ana Marçalo, Alfredo López, Vasilis Valavanis, José V. Vingada and Graham J. Pierce.

Conceived and designed stranding networks: PC, JAM-C, MF, AL, JVV

Performed the necropsies/sampling: ALL, PC, JID, JAM-C, MF, JS, HA, AM, AL, JVV.

Designed the analysis: GJP and ALL

Analyzed the data: ALL.

Contributed reagents/materials/analysis tools: AL, JVV, VV, GJP.

Wrote the paper: ALL.

Edited the text: GJP.

Provided constructive comments on the manuscript and approved the final document: GJP, AL, JVV.

Abstract

Strandings are an important source of information and biological samples which can provide useful insights into the conservation status of coastal cetacean populations. Harbour porpoise stranding data used in the current study (N=424) were recorded from 1990 to 2013 by Coordinadora para o Estudo dos Mamíferos MAriños (CEMMA) in Galicia, and from 2000 to 2013 by Sociedade Portuguesa de Vida Selvagem (SPVS) in Portugal. The West Iberian Peninsula (WIP) is an area of high fishing effort, leading to a level of cetacean by-catch that is suspected to be unsustainably high.

Strandings occur throughout the year. In Galicia porpoise strandings were more common in winter with a peak in March and in April; and in Portugal a peak in May was detected. There was a generally increasing trend in the number of stranded porpoises from North to South with peaks in subareas 5 and 9 (Ría de Pontevedra and Figueira da Foz). Numbers stranded also varied year to year, with a generally increasing trend over time. Areas with highest occurrence of strandings did not correspond to the areas with the highest number of sightings. Other factors may influence the presence of carcasses in the coast, e.g. seasonal currents and seasonal fishing activity.

The sex ratio among strandings was close to 1:1 although there was a slight preponderance of females in Portugal. Body length ranged from 81 to 202 cm (mean 146.7 cm), with Portuguese porpoises being larger than Galician, and females larger than males. Overall, 33.4% of the stranded porpoises had signs of by-catch, with a higher proportion in Portugal (56.0%) than in Galicia (26.2%). This difference may reflect differences in fishing gears used in each area but there results support the previous suggestion that the bycatch rate is unsustainably high and indicate that this differentiated and isolated harbour porpoise population of the WIP faces an important problem. As the WIP an area with a strong dependence on fisheries, it may be very difficult to eliminate cetacean by-catch. However, measures to reduce that problem and specific management plans for porpoises should be developed.

Introduction

There are several reasons why European Seas are not considered to be in "good environmental status" (GES) (European Commission 2014): i) an increasing pressure from human activities, ii) 39% of fish stocks in the Northeast Atlantic are still overfished and the situation is improving slowly, iii) pollution, iv) marine litter (mostly plastic), and, v) climate change. The Marine Strategy Framework Directive (MSFD) requires achievement of GES in EU marine waters by 2020. There are many indicators defined to detect if that goal is achieved, some of which relate to the distribution, abundance and population dynamics of cetaceans. To assess the status of these populations, if conservation measures are needed and their effectiveness in the future, it is essential to have long time-series of relevant data to help identify baseline conditions (Evans et al 2005, ICES 2013).

Collection of the necessary data on cetaceans is difficult because they are highly mobile species, spend a lot of time below the sea surface (e.g. Redfern et al 2006, Kiszka et al 2007) and away from areas used regularly by humans, especially those species occurring predominantly offshore. There are different techniques to study the presence, distribution and abundance of cetaceans, such as boat, aerial, land-based and acoustic surveys (for a review, see Evans and Hammond 2004). Another approach is the study of strandings, which can be of dead or live animals. They are an important source of information and biological samples. Stranding data collection has low costs comparing to field work at sea, even if necropsies are carried out, and data collected can be from a wide spatial and temporal range. In addition, for some countries, good historical data series exist. Strandings data can provide a good indicator of the species present in an area (Maldini et al 2005, MacLeod et al 2005, Pyeson 2010, 2011). Also, spatiotemporal trends in distribution, migrations, abundance and population dynamics (e.g. mortality rate) can potentially be detected (Sequeira et al 1996, López et al 2002, Siebert et al 2006, Ferreira 2007, Leeney et al 2008, Pikesley et al 2011, Ferreira et al 2012, Truchon et al 201), which could be related to human activities such as fishery by-catch or pollution (e.g. Jefferson and Curry 1994, Sequeira 1996, Siebert et al 1999, Bennet et al 2001, Jauniaux et al 2002, Jepson et al 2003, Das et al 2004 b, Healters and Camphuysen 2009, Mahfouz et al 2014 a, b), anthropogenic noise (Simmonds and Lopez-Jurado 1991, Frantzis 1998, Balcomb and Claridge 2001, Jepson et al 2003, 2005, Fernández et al 2004, 2005, 2012, Cox et al 2006), ship strikes (ACCOBAMS 2005, Panigada et al 2006, Wang et al 2006, IWC 2012) or climate change (MacLeod et al 2005).

The analysis of strandings also gives information about health (e.g. condition, diseases, parasites) and causes of mortality, and about life history in general (Lockyer et al 2001, Lockyer 2003, Lockyer and Kinze 2003, López 2003, Murphy 2008, Murphy et al 2009, Lopez et al 2012, Read et al 2012, Learmonth et al 2014) as well as other aspects of biology and ecology such as diet (e.g. Santos and Pierce 2003, Das et al 2003, Santos et al 2004, 2005, De Pierrepont et al 2005, Tonay et al 2007, Aguiar 2013, Dunshea et al 2013), contaminants (e.g. Aguilar et al 1999, Jepson et al 2005, Pierce et al 2008, Murphy et al 2010, Méndez-Fernández et al 2014 a, b) or genetics (e.g. Ju et al 2012, Amaral et al 2012 a, b, Defaveri et al 2013, Stockin et al 2013, Fontaine et al 2014). Monitoring strandings also makes it possible to detect any change in these characteristics (Lockyer and Kinze 2003, López 2003, Murphy 2008, Murphy et al 2009, López et al 2012, Read et al 2012, ICES 2013, Truchon et al 2013, Byrd et al 2014), and provide insights on the fitness and survival of the population.

Nevertheless, it is important to keep in mind that strandings are an opportunistic source of information. Aside from possible variation in observer effort along the coast, which can affect the probability of beached animals being detected, environmental factors such as, winds, sea-pressure gradients, tides, currents and/or bottom topography can affect the probability of dead cetaceans reaching the shore and stranding (Evans et al 2005, Leeney et al 2008, de Boer et al 2012, Peltier et al 2012, 2013). Previous studies have analysed the proportion of carcasses that strand by tagging by-caught animals or animals found floating in the sea. Results showed different but generally low stranding rates: none of four cetaceans tagged and released were reported on the coast of Southwest England (de Boer et al 2012), only 8 of 100 tagged animals reached land in the French Atlantic (Peltier et al 2012) and 5 of 23 in Galicia (Martinez-Cedeira et al 2011).

Also, Peltier et al (2012) used the drift model MOTHY developed by *MétéoFrance* to link stranding locations to likely areas of origin, considering the effects of wind and tide but not general circulation or coastal currents. Their results suggest that only a small fraction of cetaceans that die over the continental shelf are stranded but conclude that stranding data could nevertheless provide relevant information on mortality at sea, relative abundance, species richness and distribution of cetaceans.

This study is focused on the West Iberian Peninsula (WIP), which comprises Galicia (Northwest Spain) and Portugal. In Southern Galicia, beaches cover 13.8% of the coast, but the Northern coastline is mostly rocky and shallow. In northern Portugal, a rectilinear sandy coast extends to just north of the Nazaré Canyon, interrupted only by Cape Mondego. Further south, beaches

are replaced by cliffs which extend to Cape Raso, at the latitude of Lisbon (OSPAR 2000). The most irregular section of the WIP is Galicia, which contains many rías. The rías are flooded tectonic valleys of moderate depth. At mouths of the Rías Baixas (the rías of Vigo, Pontevedra and Arousa, in south Galicia) there are the archipelagos of Cíes and Ons, and Sálvora Island. The rías form an intrinsic component of the "shelf system" (Doval et al 1998), the oceanographic characteristics of which are driven by large scale and local winds, especially during summer when freshwater input is at its minimum.

The WIP is characterized by a relative narrow shelf of 20 - 35 km wide and 100 – 200 m depth, with two principal currents present: i) the Portuguese Current, a broad equatorward current, and ii) the Navidad Current (Pingree and Le Cann 1989), a branch of the Iberian Poleward Current IPC that enters the Cantabrian Sea. The area is also the northern limit of the NW African upwelling system. Upwelling on the Galician and Portuguese shelf is seasonal and is caused by northerly winds during summer and Eckman transport (e.g. Fraga 1981, Prego and Varela 1998, Figueiras et al 2002). Upwelling is also associated with the IPC (Alvarez et al 2003), and the interaction of coastal upwelling and strong outflow from the rías generates eddies in the slope poleward flow, which could contribute to breakdown of the Iberian Polar Current (IPC) during the start of the upwelling regime (Torres and Barton 2007). In the North WIP, eddies are also a topographic feature of the coast in areas such as the Estremadura Promontory, the Aveiro Canyon and the Porto Canyon (Peliz et al 2003). Results of a 10-year simulation study of Lagrangian transport pathways, showed that particles released in surface waters (1 - 10 m) from Azores, Madeira and Canary Islands follow a westward propagation of the Canary Current, while particles released at the Iberian coast travelled southwards probably due to the Portugal Current (PoC) which joins the North Atlantic Current. However, particles released along the western coast of Galicia travelled eastward toward the Cantabrian Sea, probably due to the Navidad Current (Sala et al 2013). The rías form a semi-closed system because of the downwelling winds, the presence of the poleward flow and the upwelling that takes place inside them (Torres and Barton 2007).

These oceanographic processes are important especially due to the associated enrichment of the waters, which favours biological production (e.g. Cabanas 1999, Âmbar 2002), and therefore may be good for the development and aggregation of fish and, through the food chain, for marine mammals and birds. Indeed, the WIP is a high biodiversity area with almost 400 species of fish (Bañón et al 2010) and over 75 species of cephalopods (Guerra 1992). Also, at least 22 species of cetaceans have been recorded in Galicia (Penas-Patiño and Piñeiro 1989,

López el al 2002, López 2003, Covelo et al 2009) and 16 species of cetaceans in Portugal (Brito et al 2009, Ferreira et al 2012), with the common dolphin (*Delphinus delphis*) the most common species followed by bottlenose dolphin (*Tursiops truncatus*) (in Galicia) or harbour porpoise (*Phocoena phocoena*) (in Portugal).

The area's resources are used by fishermen and cetaceans and it is an area of high fishing effort (Sequeira et al 1992, EUROSTAT 2010), leading to a level of cetacean by-catch that is suspected to be unsustainably high (López et al 2012, Read et al 2012, Goetz et al 2014).

In the study area there are two strandings monitoring networks. In Galicia, strandings began to be recorded from 1973 by the Sociedade Galega de Historia Natural (SGHN), with recording becoming systematic in 1990 with the creation of the Coordinadora para o Estudo dos Mamíferos Mariños (CEMMA) which, since 1999, has had an agreement with the Xunta de Galicia for the management of the official stranding network for marine mammals and turtles in Galicia. In Portugal, the National Stranding Network, which joined the Aquário Vasco da Gama, Museu do Mar (Cascais) and the Autoridade Marítima, was created in 1977. At the end of the 1980s, the coordination passed to the Serviço Nacional de Parques, Reservas e Conservação da Natureza (currently ICNF). Due to the high number of strandings along the coast of central Portugal, in 2000 a local stranding network was created by the Universidade do Minho (UM) in collaboration with the Sociedade Portuguesa de Vida Selvagem (SPVS) and the Instituto da Conservação na Natureza e da Biodiversidade (ICNB), belonging to the National Stranding Network managed by the ICNF. Since 2008, this local stranding network for marine mammals, turtles and birds, has also worked in the North part of Portugal and the Algarve area.

Stranding data recorded in Galicia and Portugal were useful to begin the validation of the status of *P. phocoena* in that area with previous studies as to provide information on the biology and ecology of porpoises in this area. (Sequeira 1996, Lens 1997, Lopez 2003, Read et al 2012, Lopez et al 2012). In the present study data from 1990 to 2013 by CEMMA in Galicia, and from 2000 to 2013 by SPVS in Portugal, for harbour porpoise, were analysed to detect i) spatiotemporal patterns and the possible presence of peaks (locations, years, months) in strandings, ii) changes in length composition and sex ratio, and iii) proportion of porpoises by-caught. In addition, the analysis aims to quantify the effect of several variables such as year, month, location (SA), body condition (bc), length, sex, by-catch on length composition, sex ratio and by-catch rate and to compare trends in strandings with those seen in sighting data from boat and land-based surveys.

The intent is to increase our knowledge on WIP porpoises. The comparison of the results with sighting data will highlight if any increase/decrease in the number of strandings may be due to differences in local abundance. Results on length composition and sex ratio will also help to describe the structure of the population in this area.

Understanding variation in population structure in time and space, together with variation in by-catch, is especially important to study in this species, which is protected by several international agreements and directives such as ASCOBANS (Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas), ACCOBAMS (Agreement on the Conservation of Cetaceans in the Black Sea, Mediterranean Sea and Contiguous Atlantic Area), and the Habitats Directive. The Iberian population has been described as genetically isolated from porpoises in the rest of Europe (Fontaine et al 2007, 2014, see also Chapter II). Also, as a top predator and a long-lived species, porpoises feed at high trophic levels and thus accumulate relative high levels of contaminants and, as the smallest resident cetacean species, carrying relatively small energy reserves, it may be particularly vulnerable to the effects of environmental changes (MacLeod et al 2014). The findings will be relevant for the implementation of the MSFD and for the conservation of the marine environmental and the species in WIP.

Materials and methods

Stranding data collection and study area.

Since 1990 the NGO Coordinadora para o Estudo dos Mamíferos Mariños (CEMMA) has recorded marine mammal and sea turtle strandings occurring on the Galician coast, but the coverage of the stranding network has been more consistent since 1999 because of the agreement with, and funding from, the Xunta de Galicia, the regional government. In Portugal, in the North, Central region, and Algarve area, the organisation Sociedade Portuguesa de Vida Selvagem (SPVS) has worked on strandings since 2000. Samples obtained are stored (in sample banks) for further biological studies (e.g. diet, life history, contaminants, genetics, etc) and annual reports are sent to the Galician and Portuguese Governments, respectively.

Strandings are reported to a dedicated phone number, available 24 - 7, and reports came from a variety of sources, including the public and local municipalities.

Cetaceans were considered stranded if they were found on the shore, either dead (either on land or in the water) or alive but in need of human intervention. Carcasses brought ashore by fishermen were also included in the study (seven in Galicia).

For each stranding, standard data (e.g. date, place of stranding/geographic coordinates, who reported the stranding, species, length, sex, body condition, cause of death such as by-catch, pneumonia/septicaemia, trauma, when possible) and additional data (e.g. morphometrics, samples collected, presence of parasites, by-catch signs, mutilations) were collected when possible according to established protocols (Kuiken and García Hartman 1992).

For the study of fisheries interactions, animals found in good condition were classified as i) not by-caught; ii) possibly by-caught, if there were suspicious lesions that could not be identified definitively as due to by-catch; iii) by-caught, animals with evidence of entanglement lesions, mutilations, or which were landed by fishermen; or, iv) unknown. When possible, the fishing gear was recorded (gillnets, trammel, trawl nets and seine). Due to carcass decomposition (body condition 4 and 5), some evidence of by-catch will have been lost. Because of this and the absence of signs in some cases or presence of ambiguous signs, the number of animals by-caught may be under-estimated. Also, it may be an overestimation due to dead animals being caught in nets and acquiring by-catch signs post-mortem, or those animals brought by fishermen to land.

If some or all this information was not recorded, cause of death was classified as NA (not available).

Data analysis and modelling.

Stranding data from January 1990 to December 2013 from Galicia and from April 2000 to December 2013 from Portugal were compiled from the CEMMA and SPVS databases.

For analyses, each stranding was considered a separate event. For harbour porpoises, no mass strandings (i.e. stranding of 2 or more individuals, excluding mother–calf pairs of the same species, at the same location on the same day) or mother-calf pairs were reported.

For statistical analysis of spatial patterns, the coastline has been divided into 10 sub-areas that are shown in Fig. 39.

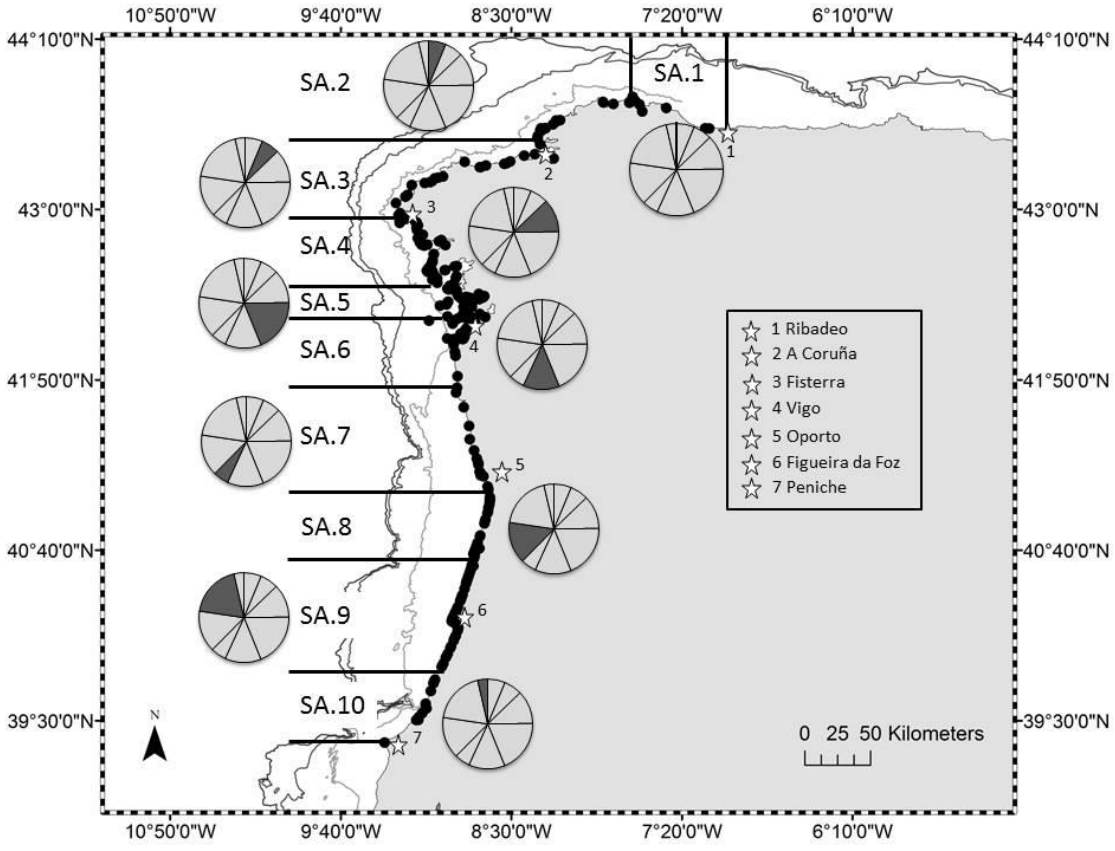


Figure 39. Distribution of the harbour porpoise strandings along the coasts of Galicia and Portugal. Black dots represent each stranding, pie charts represents the proportion of strandings in each sub-area filled in dark grey .

Animals without the head or fluke (due to amputation, predation or decomposition) were not considered for the analyses of body length trends. Data from porpoises with body condition of 4 and 5 were also not considered for analyses of by-catch, length or sex.

A chi-squared analysis was used to compare monthly trends between Galicia and Portugal.

Due to the differences in strandings datasets from the two areas, for most analyses data were separated into two groups: i) Galician data from 1990 to 2013; and, ii) data from Galicia and Portugal from 2000 to 2013.

For the analysis of the effects of different covariates (year, month, sub-area, body condition, length, sex and by-catch) on harbour porpoise strandings, Generalised Additive Models (GAMs) were fitted as they permit non-normal distributions of response variables (discrete or continuous) and non-linear relationships between covariates and the response variable, which are described with non-linear smooth functions (Hastie and Tibshirani 1990).

In this study, number of strandings was first modelled as a function of year, month and sub-area (SA) (all fitted as smoothers) to quantify the spatiotemporal trends in porpoise strandings. Two-way interactions between effects of subarea, year and month were also investigated. A Poisson distribution was selected for the response variable (number of porpoise strandings) and a log link function was used.

Secondly, a model was fitted to quantify the effects of year, month, SA (as smoothers), by-catch and sex (as factor) on body length. In this case, the distribution selected for the response variable length was Gaussian with an identity link function. The same explanatory variables (except for sex) were used to study the sex of porpoises stranded, with the effect of length also included (as a smoother); in this case the distribution for the response variable was binomial with a logit link function. Finally, a model was fitted to quantify the effects of year, month, SA, length, body condition (as smoothers) on occurrence of by-catch. The response variable was transformed into presence/absence assuming that the presence of signs of by-catch implies that the animal was caught by a fishing gear, then presence included categories ii) possibly by-catch and iii) by-catch; therefore, the distribution used was Binomial with a logit link function.

To describe the characteristics of the porpoises stranded the effects of year, month, SA, bycatch and sex on body length; the effects of year, month, SA, bycatch and body length on sex and effects of year, month, SA, bycatch and sex on body length; the effects of year, month, SA, sex and body length on bycatch, were analysed.

Covariates SA and body condition were fitted as smoothers and degrees of freedom (k) were limited to k=4 and k=3 respectively, to allow a smooth curve to be fitted as they have few unique values (Zuur et al 2007).

Results

Spatiotemporal trends in Galicia from 1990 to 2013.

There is variation between years in the number of strandings of harbour porpoises in Galicia (Figure 40). The year with most strandings was 1999 and the one with least was 2001. The mean is 10.12 strandings per year (S.D. 4.68).

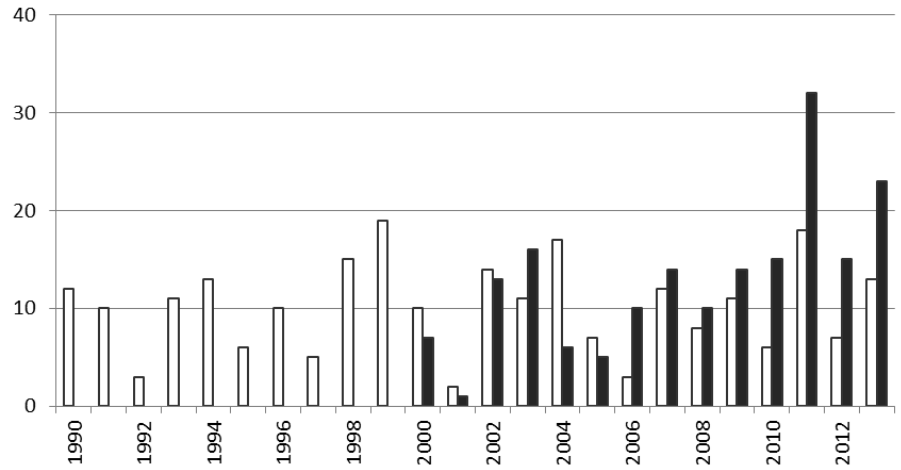


Figure 40. Number of porpoise strandings per year in Galicia (white bars) and Portugal (black bars). The absence of data from Portugal before 2000 is due to the beginning of the Stranding Network in that year.

Differences between months were also detected, with a lower number of strandings from May to October. The mean number of strandings per month per year during that period was 1.41 (S.D. 7.8), for the remaining months (from January to April, November and December) the mean number of strandings per month per year was 1.52 (S.D. 0.45). Most strandings were detected in March and April, and the least was in September.

If the number of strandings is analysed by sub-area (SA), it increases from North (SA.1) to South (SA.6), with the largest number of strandings found in SA.5.

Model	Explanatory variables								Desv. Expl.	AIC
	Year	YEAR, by = as.factor (MONTH)	YEAR, by = as.factor(SA)	Month	as.factor (MONTH)	MONTH, by = as.factor(SA)	SA	as.factor (SA)		
Y1~ 1 + s(YEAR) + s(MONTH) + s(SA, k = 4)				***, ∩U (4.55)			***, + (2.39)		11%	1393.92
Y2 ~ 1 + as.factor(MONTH) + s(YEAR, by = as.factor(MONTH)) + s(SA, k = 4)					***		***, + (2.39)		19%	1389.63
January		*, + (1)								
April		** (7.75)								
June		. (3.83)								
October		* (4.43)								
December		**, - (1)								
Y3 ~ 1 + as.factor(SA) + s(YEAR, by = as.factor(SA)) + s(MONTH)				*** (4.55)				***	17%	1377.68
SA.2			·, + (1)							
SA.3			** (8.75)							
SA.5			*** (4.37)							
Y4 ~ 1 + as.factor(SA) + s(MONTH, by = as.factor(SA)) + s(YEAR)								***	17%	1372.47
SA.2						* (3.43)				
SA.4						***, U (7.62)				
SA.5						*** (6.78)				
SA.6						**, - (3.17)				

Table 16. GAM models fitted for stranding data from Galicia 1990 - 2003 to study spatiotemporal variation, and p-values. (Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1), trends ('+' positive, '-' negative, 'U' with a minimum, '∩' with a maximum) and degrees of freedom (in brackets). Explanatory variables analysed are: year, month and sub-area (SA).

GAM models were fitted to quantify the effects of year, month, sub-area, body condition, length, sex and by-catch covariates on the number of strandings. In a first model (Table 16 Model Y1), the covariates year, month and SA were included and we found that only year was not significant. In Figure 41 it can be seen that a negative trend was found in the number of strandings by month from March to August; and that the number of strandings increases from North (SA.1) to South (SA.5). However, the picture becomes more complicated when interactions between the covariates are considered.

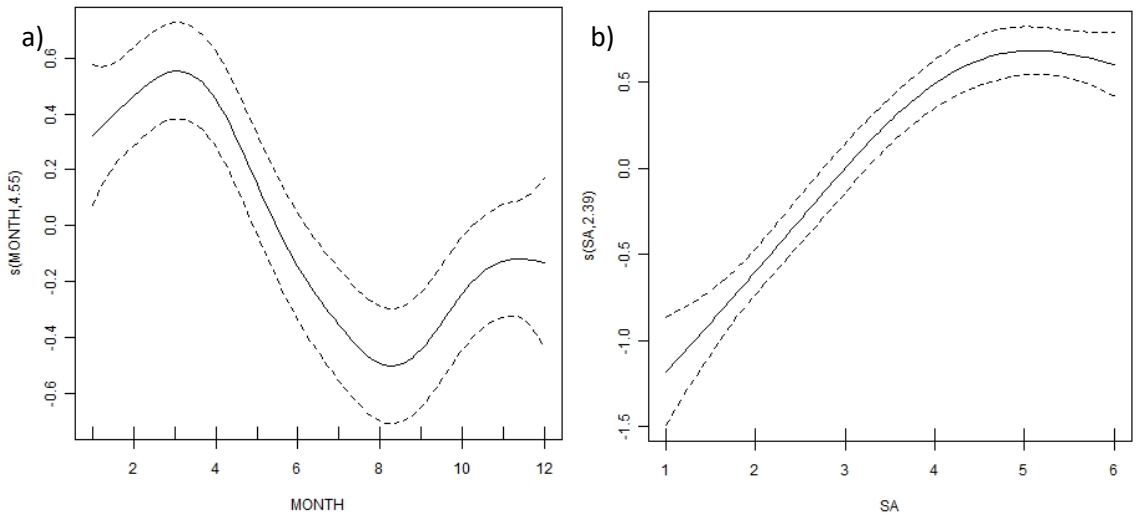


Figure 41. Graphs showing the effects of the significant covariates in the GAM fitted for Galicia to model the spatiotemporal trends in the number of strandings (year, month and subarea, as SA). Model Y1. Significant covariate a) month and b) sub-area (SA).

In the model with year effects fitted separately for each month (Table 16 Model Y2, Fig.42), a significant effect of the year was found for several months. A positive trend was found in January, and a negative trend in December. Years with a higher proportion of strandings in April are 1990, 2004 and 2011. In June, the number of strandings decreased since from 1997 until 2005, when it began to increase. A similar interannual pattern of strandings was found in October; the strandings decreased from 1999 until 2009. The covariate SA had a positive trend, with more strandings in southern than northern sub-areas. A significant effect on strandings was also found for the covariate month when fitted as a factor.

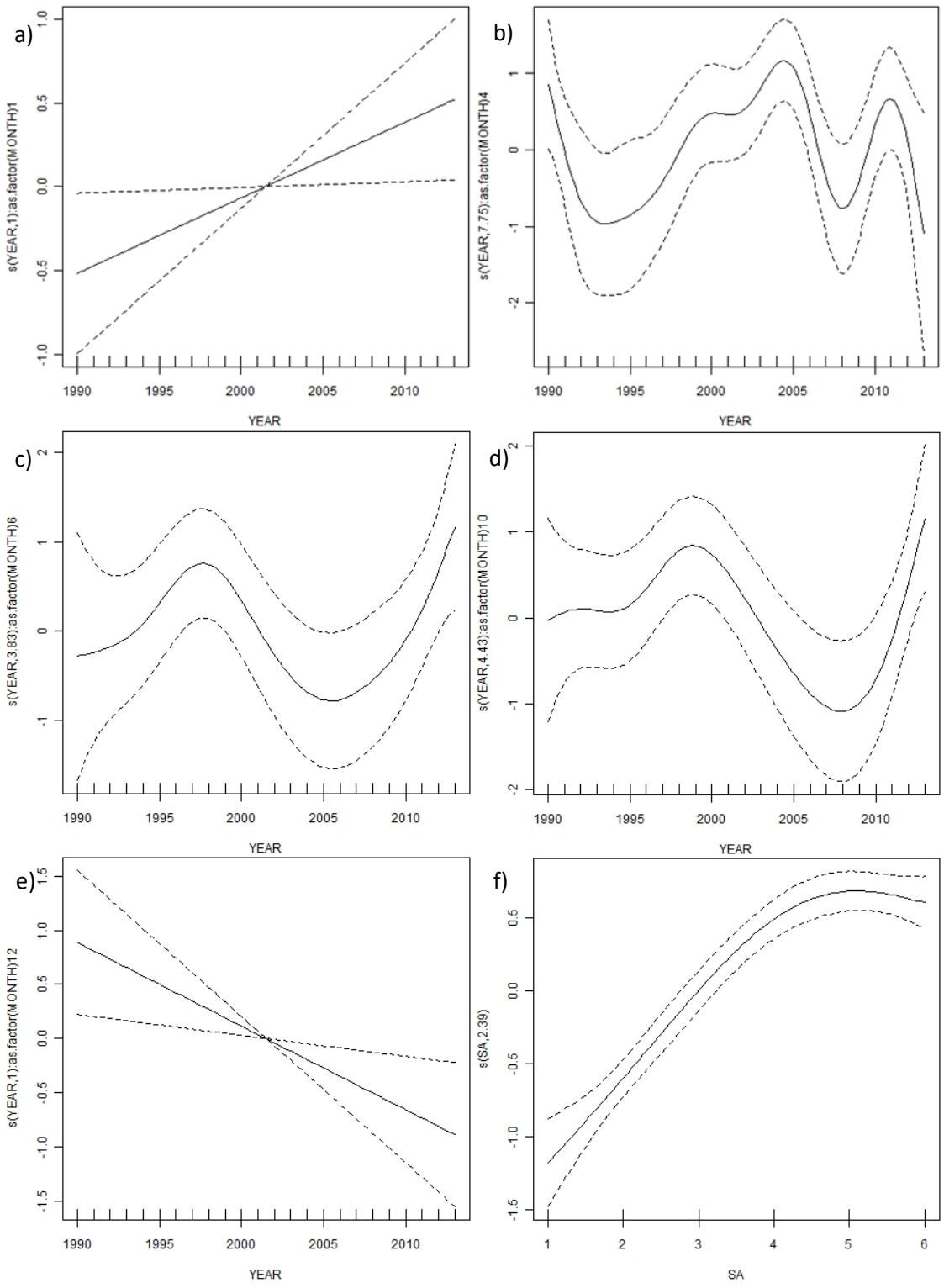


Figure 42. Graphs of the significant covariates of the GAM fitted for Galicia to model the effects of year, month and SA on porpoises strandings. Model Y2. a) Covariate year in January, b) covariate year in April, c) covariate year in June, d) covariate year in October, e) covariate in December, f) covariate sub-area.

Significant effects of year and month were seen for some sub-areas. When the effect of the year is modelled by sub-area (Table 16 Model Y3 Fig. 43) it can be seen there was a positive year on year trend in the number of strandings in SA.2. For SA.3 the number of strandings decreased markedly from 1994 to 1997. For SA.5, there was a peak in 2000, and lowest numbers were found around 2008. The effect of month in the model was similar to that in model Y1. A significant effect was also found when SA was fitted as a factor.

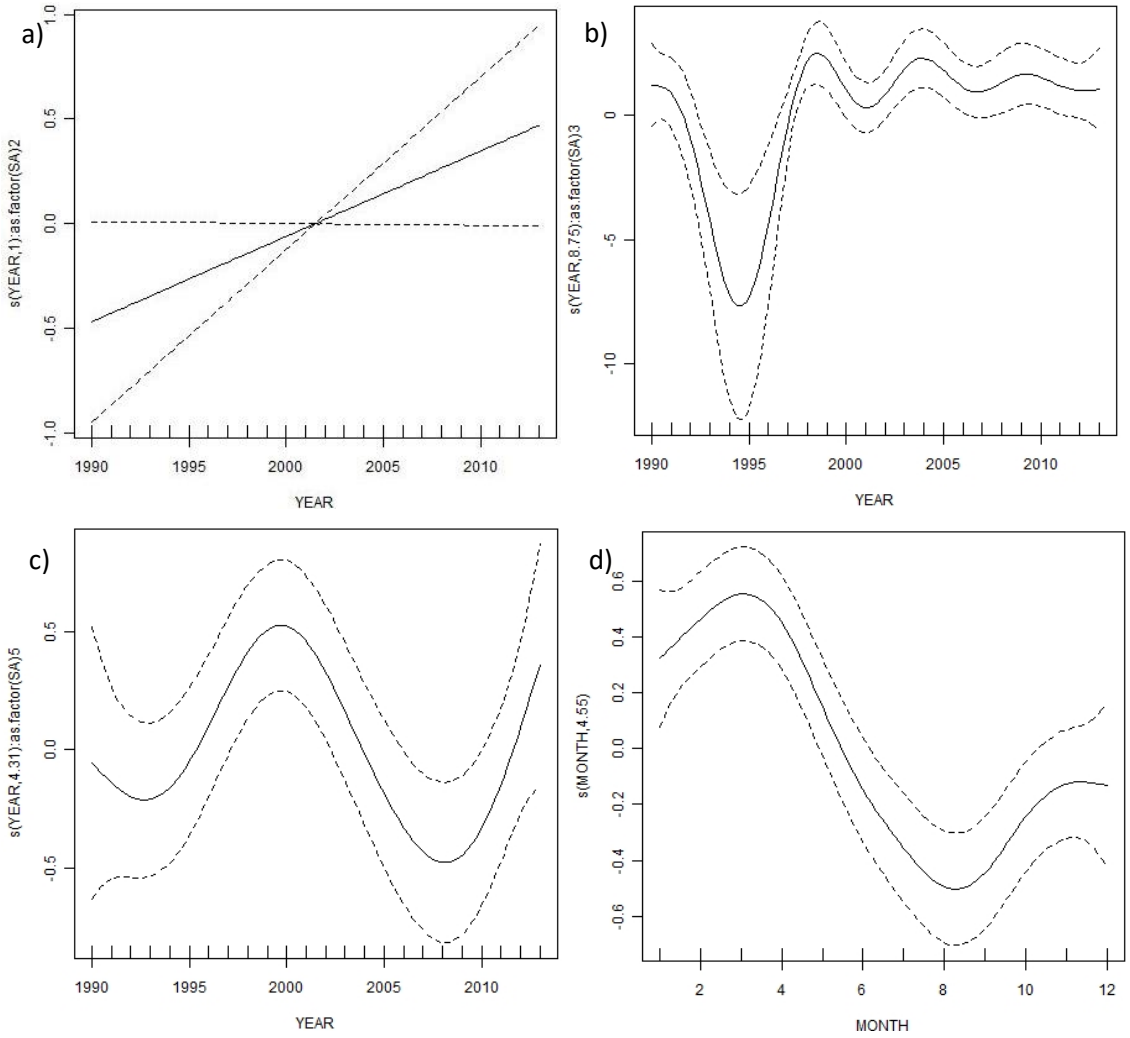


Figure 43. Graphs of the significant covariate of the GAM fitted for Galicia to model the effects of year, month and SA on porpoise strandings. Model Y3. a) Covariate year in SA.2, b) covariate year in SA.3, c) covariate year in SA.5, d) covariate month.

When modelling the effect of month in each sub-area (Table 16 Model Y4, Fig. 44), there is a maximum in the number of porpoise strandings in March, after which it decreases to a minimum in September. A similar distribution was found in SA.5, but reaching the minimum one month earlier (August). In contrast, in SA.4, there is a decrease in the number of

strandings from January to June when there is a minimum and a peak in July and October. In the southern area of Galicia (SA.6) a peak was seen in April. The effect of year was not significant in this model; in contrast, SA (as a factor) was highly significant.

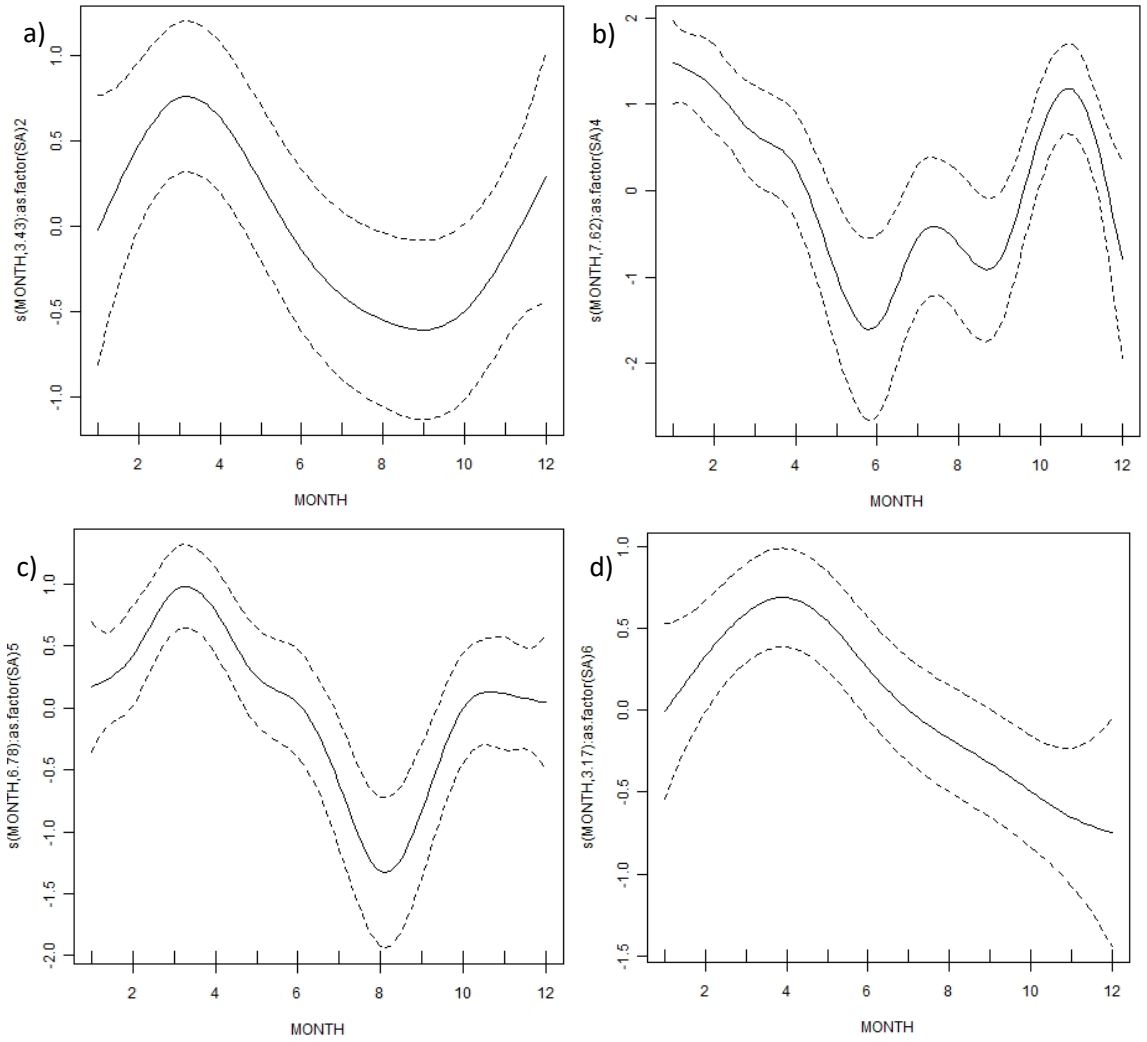


Figure 44. Graphs of the significant covariates of the GAM fitted for Galicia to model the effects of year, month and SA on porpoise strandings. Model Y4. a) Covariate month in SA.2, b) covariate month in SA.4, c) covariate month in SA.5, d) covariate month in SA.6.

Spatiotemporal trends in Galicia and North Portugal.

For the period of 2000 - 2013, there is significant variation between years in the number of strandings of harbour porpoises both for Galicia and North Portugal ($\chi 2=79.32$, d.f.=13, $p<0.001$) (Fig. 40), with an evident increase in the number in 2011 and 2013 in Portugal. The year with the highest number of strandings in both areas is 2011 and the one with fewest is 2001. The mean number of strandings per year is 9.93 (S.D. 4.76) for Galicia, 12.93 (S.D. 7.80) for North Portugal, and 22.86 (S.D. 11.2) for both areas together. This variation between years in the number of stranding of porpoises is in contrast to the one found for Galician strandings alone, and may mean that this variation is mainly due to Portuguese strandings.

There is a clear difference between months for both areas (Fig. 45). In Portugal a minimum number of strandings was found in January and maximum in May, with more strandings in summer than winter. For Galicia, more strandings were recorded in winter than summer ($\chi 2=40.20$, d.f.=12, $p<0.001$). For Portugal, mean number of porpoise strandings per month was 15.08 (S.D. 6.89), and for the whole area it was 35.33 (S.D. 7.80).

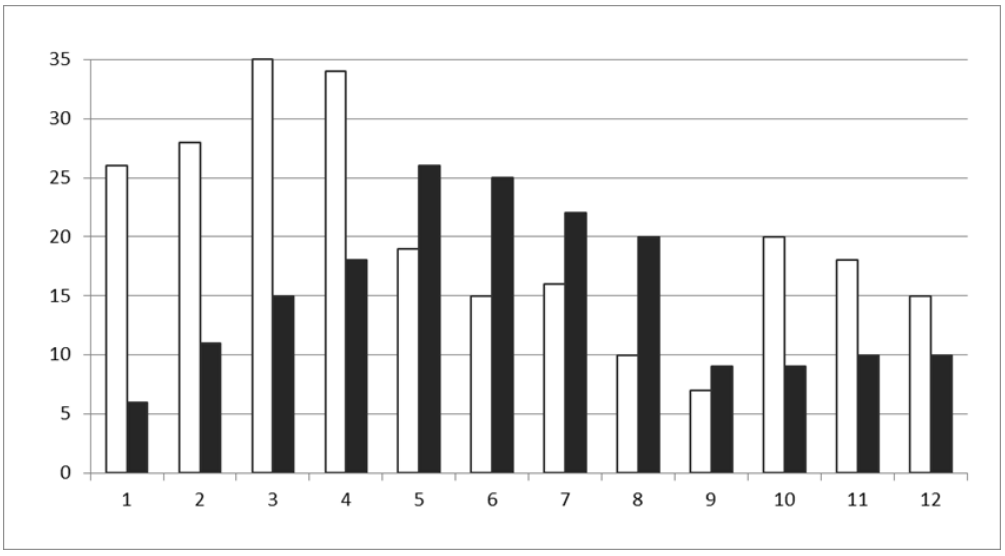


Figure 45. Number of strandings per month in Galicia (white bars) and Portugal (black bars) from 2000 to 2013.

Strandings increased from North (SA.7) to South (SA.9), with a great decrease for the last SA (Fig. 46).

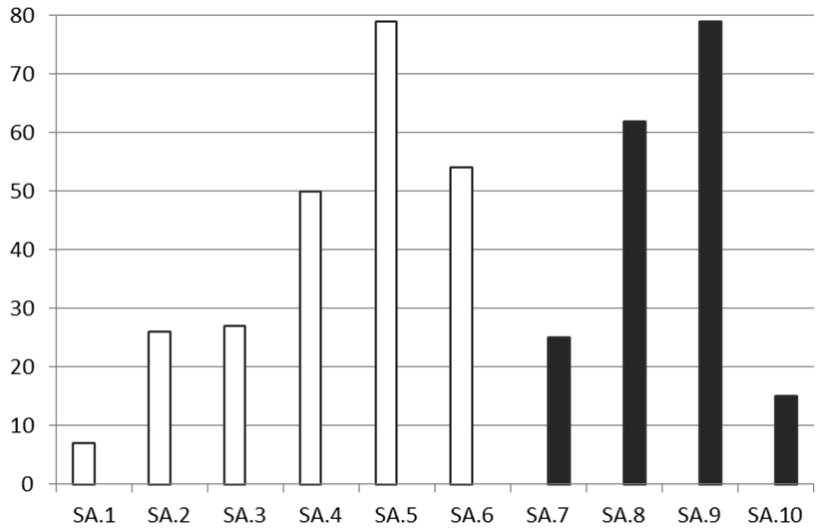


Figure 46. Number of strandings per Subarea (SA) in Galicia (white bars) and Portugal (black bars) from 2000 to 2013.

Data from both areas from 2000 to 2013 were used to fit a GAM to study the effects of year, month and SA covariates on the number of porpoise strandings (Table 17 Model Y8, Fig. 47), and it was found that all covariates were significant. The number of strandings varied significantly between years, with a peak in 2003 and maximum number of strandings found in the three last years of the study; minimum numbers were found in 2001 and 2005. There is a peak at April. The number of porpoises stranded increases from North to South.

Model	Explanatory variables								Desv. Expl.	AIC
	Year	YEAR, by = as.factor (MONTH)	YEAR, by = as.factor(SA)	Month	as.factor (MONTH)	MONTH, by = as.factor(SA)	SA	as.factor(SA)		
Y8 ~ 1 + s(Year) + s(Month) + s(SA, k = 4)	***, + (8.14)			***, ∩ (3.21)			***, + (2.29)		11.40%	1688.12
Y9 ~ 1 + as.factor(Month) + s(Year, by = as.factor(Month)) + s(SA, k = 4)					***		***, + (2.29)		18.70%	1674.69
January		*, + (1)								
April		* (6.71)								
May		**, + (1)								
June		***, + (1)								
July		*, + (1)								
October		** (3.35)								
November		* (6.16)								
Y10 ~ 1 + as.factor(SA) + s(Year, by = as.factor(SA)) + s(Month)				***, ∩ (3.21)				***	24.10%	1594.72
SA.2							., + (1.63)			
SA.4							. (4.37)			
SA.5							*** (8.68)			
SA.7							*** (7.27)			
SA.8				***, ∩ (3.21)			**, + (1)			

Table 17. GAM models fitted for stranding data from Galicia and Portugal 2000-2003 to study spatiotemporal variation, and p-values (Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1), trends ('+' positive, '-' negative, 'U' with a minimum, '∩' with a maximum) and degrees of freedom (in brackets). Explanatory variables analysed are: year, month and sub-area (SA).

Model	Explanatory variables								Desv. Expl.	AIC
	Year	YEAR, by = as.factor (MONTH)	YEAR, by = as.factor(SA)	Month	as.factor (MONTH)	MONTH, by = as.factor(SA)	SA	as.factor(SA)		
SA9				***, ∩ (3.21)			**, + (1)			
Y11 ~ 1 + as.factor(SA) + s(Month, by = as.factor(SA)) + s(Year)	***, + (8.14)								23.80%	1596.67
SA.2						·, - (1)				
SA.4						***, U (2.07)				
SA.5						** (8.55)				
SA.6						***, - (4.16)				
SA.8						***, ∩ (2.34)				
SA.9						***, ∩ (3.49)				
SA.10						·, - (1)				

Table 17. Continued.

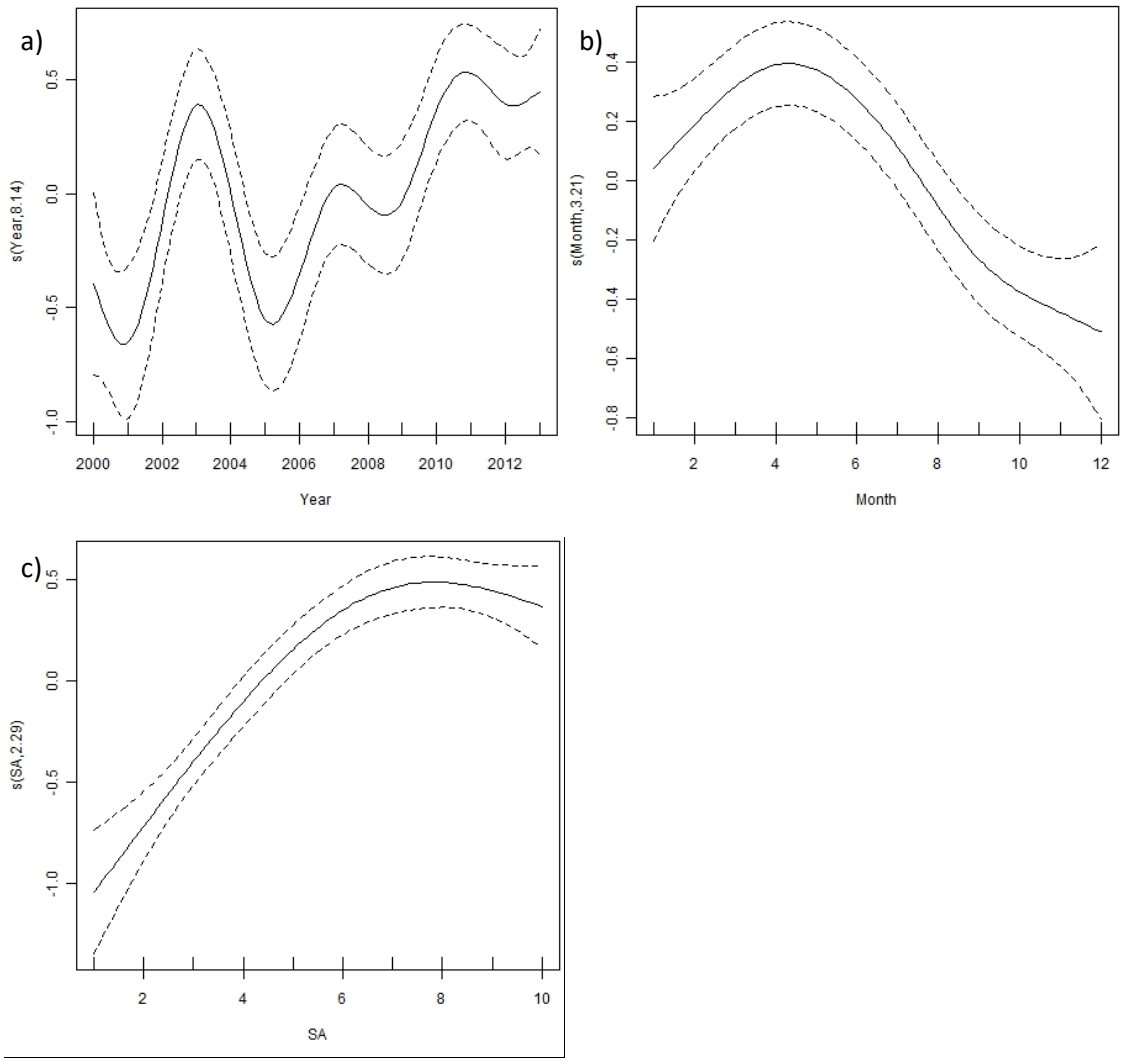


Figure 47. Graphs of the significant covariates of the GAM fitted to model the spatiotemporal trends of strandings in Galicia and North Portugal from 2000 to 2013. Model Y8. a) Covariate year, b) covariate month, c) covariate sub-area (SA).

The model with year effects fitted separately for each month for the whole area (Table 17 Model Y9, Fig. 48), showed a significant difference in the number of stranding between years for several months. There was a positive trend in January, May, June and July. In April, the number of strandings increased in 2011 after which there was a highly significant decrease in the last two years. In October, there was a minimum in the number of strandings between 2008 and 2010. In November high variation was seen, with significant differences between maxima (2002 to 2003, 2008 to 2009) and minima (2005 to 2006, 2011). Also, there was a positive effect in SA with an increase in the number of strandings of porpoises from North to South until SA.7. Month, fitted as a factor, had a significant effect on the strandings.

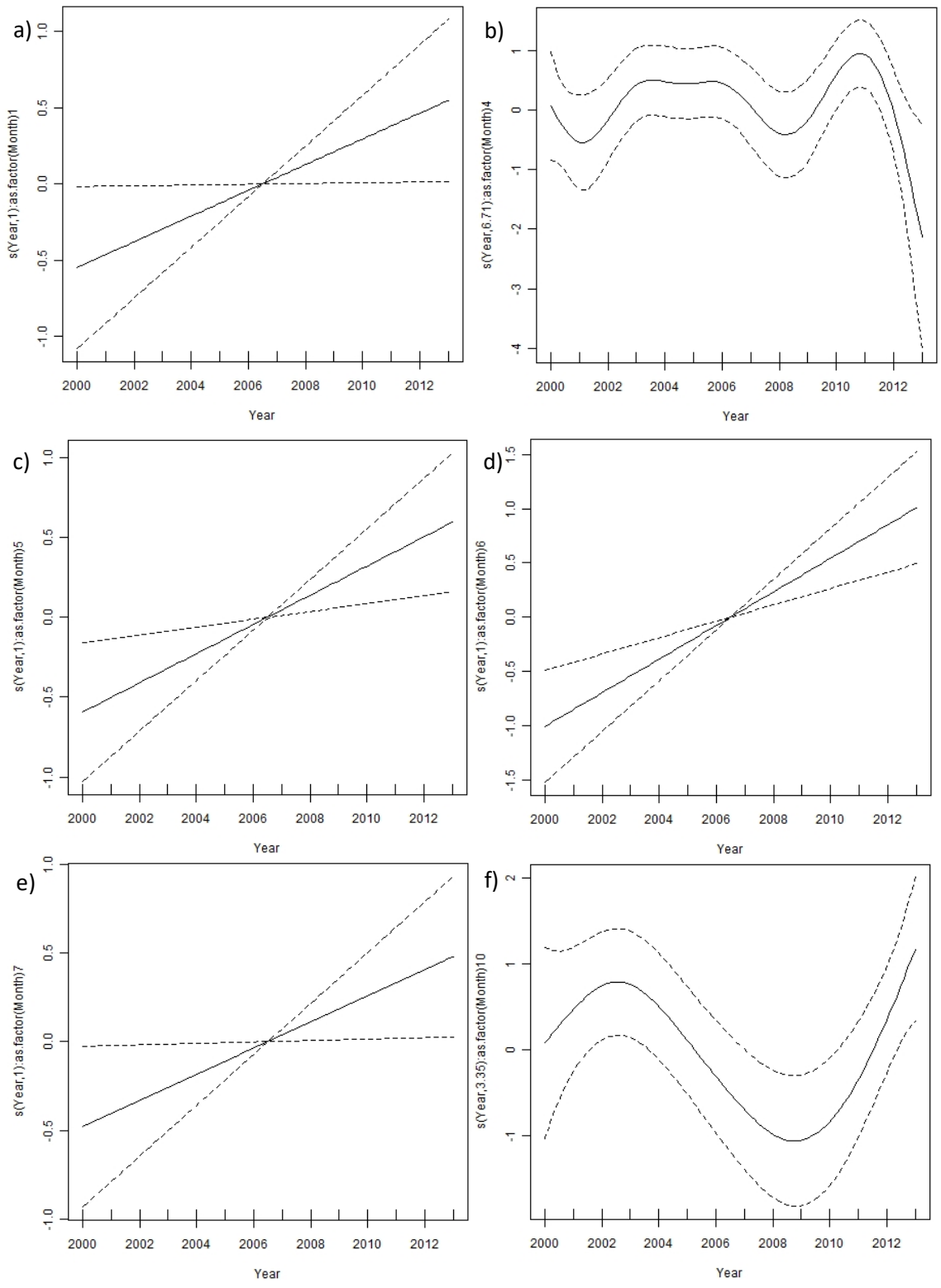


Figure 48. Graphs of the significant covariates of the GAM fitted for Galicia and North Portugal to model the effects of year, month and SA on porpoise strandings. Model Y9. a) Covariate year in January, b) covariate year in April, c) covariate year in May, d) covariate year in June, e) covariate year in July, f) covariate year in October, g) covariate year in November, h) covariate sub-area (SA).

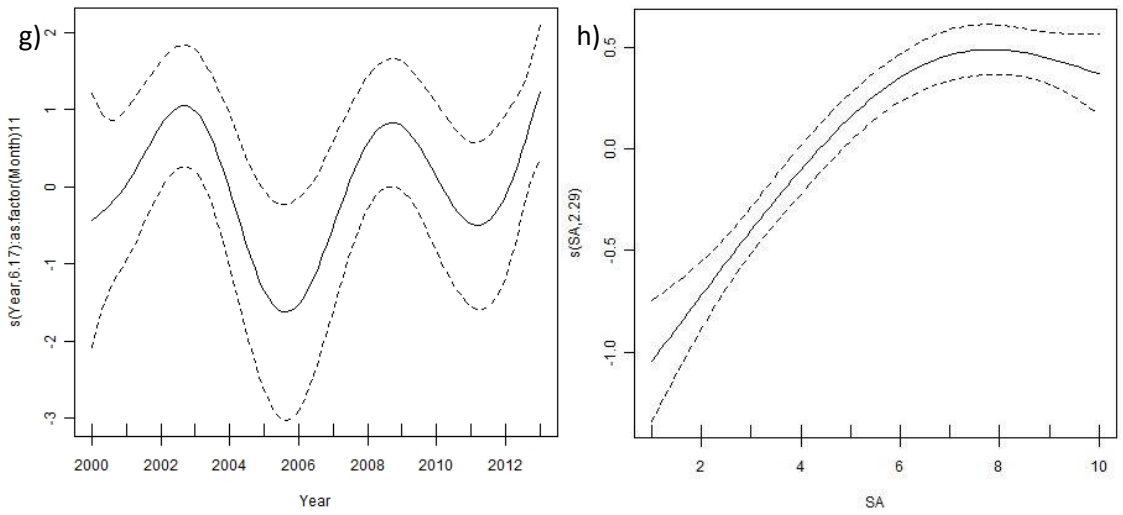


Figure 48. Continued.

Significant effects of year and month on number of porpoise strandings per sub-area were also seen for data from Galicia and Portugal (Table 17 Model Y10 and Y11, Fig. 49 and 50). The model fitting the effect of the year by sub-area (Table 2 Model Y10, Fig.49) showed a positive trend in SA.2, SA.8 and SA.9 over the study period. In SA.5, 2005, 2008 and 2012 were the years with least number of strandings. In SA.7 the number of porpoises stranded increased from 2009 until 2011. Month was found to have a significant effect with the same monthly pattern as in model Y8.

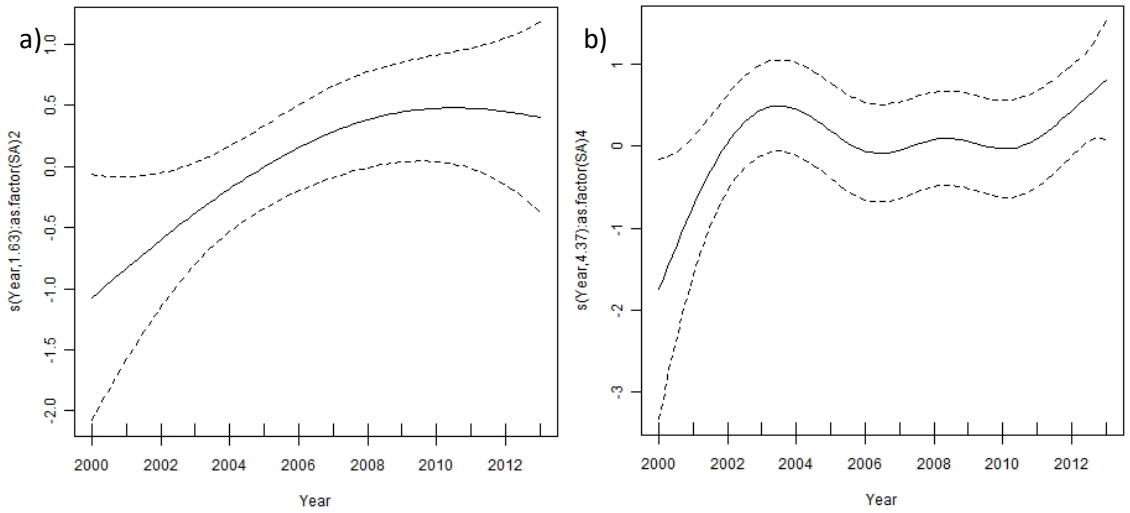


Figure 49. Graphs of the significant covariates of the GAM fitted for Galicia and North Portugal to model the effects of effects of year, month and SA on porpoise strandings. Model Y10. a) Covariate year in SA.1, b) covariate year in SA.4, c) covariate year in SA.5, d) covariate year in SA.7, e) covariate year in SA.8, f) covariate year in SA.9, g) covariate month.

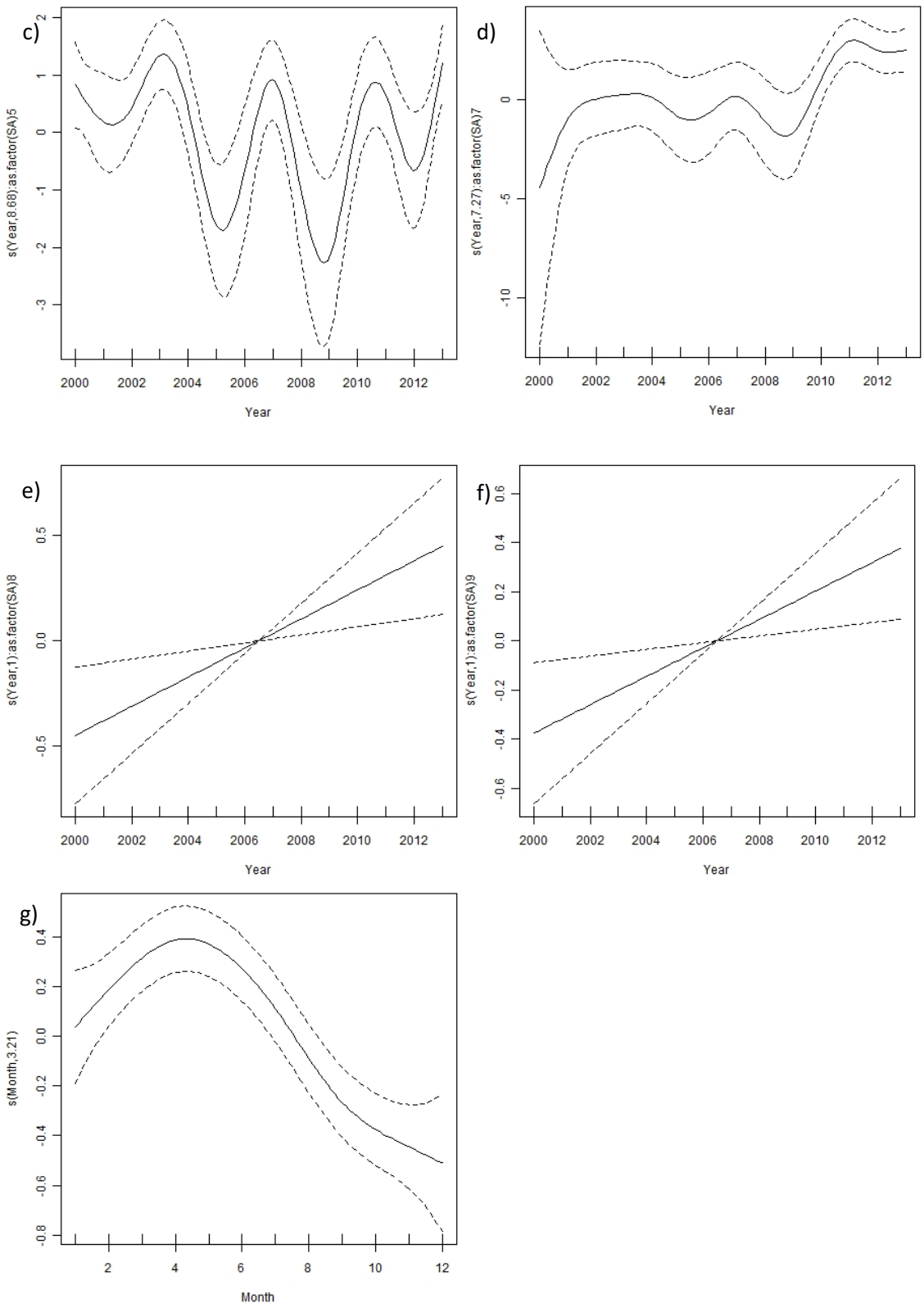


Figure 49. Continued.

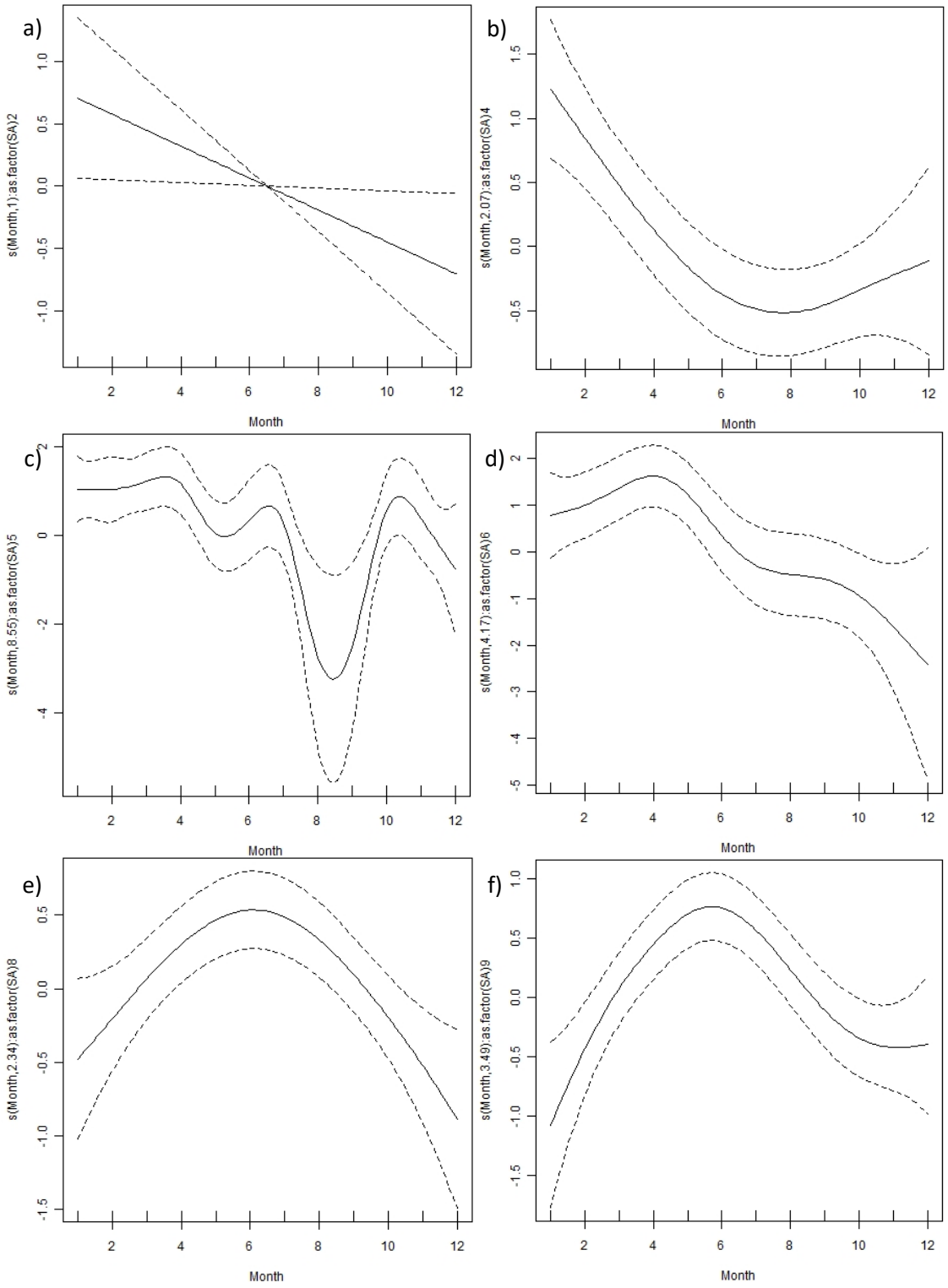


Figure 50. Graphs of the significant covariates of the GAM fitted for Galicia and North Portugal to model the effects of year, month and SA on porpoise strandings. Model Y11. a) Covariate month in SA.2, b) covariate month in SA.4, c) covariate month in SA.5, d) covariate month in SA.6, e) covariate month in SA.8, f) covariate month in SA.9, g) covariate month in SA.10, h) covariate year

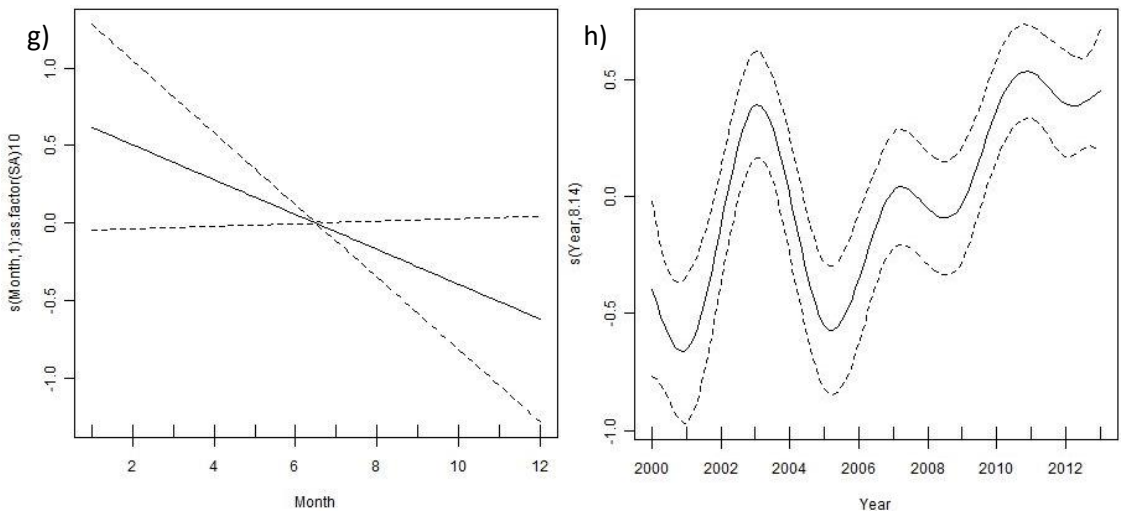


Figure 50. Continued.

The model Y11 (Fig. 50) analysed the effect of the month by sub-area. A negative trend was seen in SA.2 and SA.10, also a significant negative trend was detected in SA.4 until July. In SA.5 there was a minimum number of strandings in August. In SA.6 there was a negative trend since April. In SA.8 and SA.9 there was more number of strandings in late spring and early summer. Finally, there was a positive general trend between years, with a peak in 2003. For both models Y10 and Y 11, there was a significant effect of SA as nominal.

Trends in Length and Sex in Galicia from 1990 to 2013.

Porpoises found stranded in Galicia were from 81 cm to 202 cm length (Fig. 51), with a mean length of 145.56 cm (S.D. 25.84). A total of 60 individuals had the head or fluke amputated, so the length was not used. Also, 20 individuals with body condition 5 were not used as the length was not available or could not be assumed to be accurate.

The percentages of males and females found were similar: 45.87% were females, 44.50% were males, and 9.63% were animals for which sex was not identified. In addition, for 3 animals the sex was not available and 22 individuals had body condition 5.

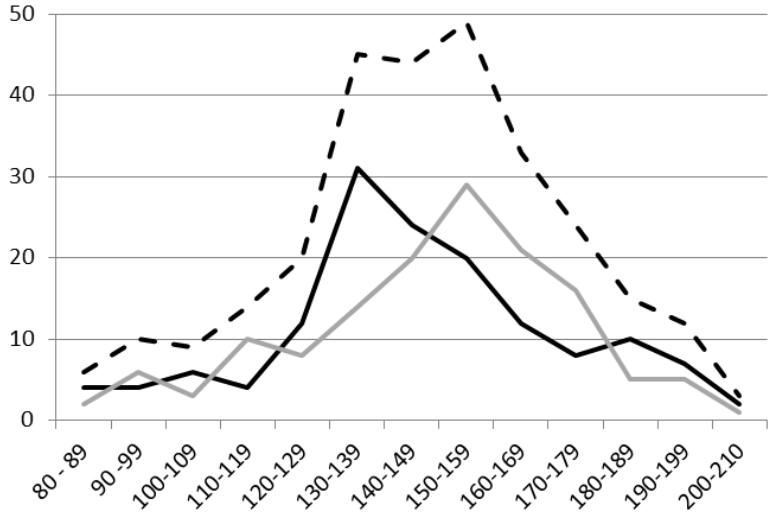


Figure 51. Number of strandings in different length classes in Galicia (black line), Portugal (grey line) and total (dash line).

Different covariates were fitted using a GAM to analyse the length of the porpoises stranded in Galicia (Table 18 Model Y5; Fig. 52): sex and by catch as factors; and year, month, SA and body condition as smoothers (with k=4 for SA and k=3 for body condition). Sex was found to have a significant effect, with males smaller than females (mean length for females: 153.03 cm (S.D. 27.35), males: 136.95 cm (S.D. 22.26)), and no significant effect was found for by-catch. A significant decrease of the length of the animals was seen through the years. A negative trend was also found at the beginning of the year, with a minimum number of strandings in May. Animals found in worse body condition were larger than animals found fresh.

The effects of year, month, SA and by-catch on sex were modelled (Table 18 Model Y6), but significant effects were not found for any of them.

Trends in Length and Sex in Galicia and North Portugal from 2000 to 2013.

Porpoises found stranded in all the studied area were from 81 cm to 202 cm length (Fig. 51), with a mean length of 146.66 (S.D. 25.49). A total of 72 individuals had some amputation that affected the measurement of the length and 33 were with body condition 5 and thus were not used. In Portugal, animals were from 84.5 cm to 202 cm length, with a mean value of 147.78 cm (S.D. 25.16).

Model	Explanatory variables								
	Year	Month	SA	Length	as.factor (SEX)	BC	as.factor (By_Catch)	Desv. Expl.	AIC
Y5 ~ 1 + as.factor(SEX) + as.factor(By_Catch) + s(YEAR) + s(MONTH) + s(bc, k = 3)	***, - (1.64)	*, U (3.23)			***	***, + (1)		35%	1316.41
Y6 ~ 1 + as.factor(By_Catch) + s(YEAR) + s(MONTH) + s(SA, k = 4)								1.48%	299.65
Y7 ~ 1 + as.factor(SEX) + s(YEAR) + s(MONTH) + s(SA, k = 4) + s(LENGTH) + s(bc, k = 3)						* (1.86)		12.3%	160.31
Y12 ~ 1 + as.factor(SEX) + as.factor(By_Catch) + s(YEAR) + s(MONTH) + s(SA, k = 4) + s(bc, k = 3)		*, U (1)	***, + (2.02)		***	**, + (1)		22.80%	1871.74
Y13 ~ 1 + as.factor(By_Catch) + s(YEAR) + s(MONTH) + s(SA, k = 4)								1.73%	388.44
Y14 ~ 1 + as.factor(SEX) + s(YEAR) + s(MONTH) + s(SA, k = 4) + s(LENGTH) + s(bc, k = 3)			*, + (1)			*** (1.92)		25.2%	237.15

Table 18. GAM models fitted to stranding data from Galicia 1990-2013 (Y5, Y6, Y7) and Galicia and Portugal 2000 - 2013 (Y12, Y13, Y14), to model length (Y5, Y12), sex (Y6, Y13) and by-catch (Y7, Y14), and p-values (Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1), trends ('+' positive, '-' negative, 'U' with a minimum, '∩' with a maximum) and degrees of freedom (in brackets). Explanatory variables analysed are: year, month, sub-area (SA), length, sex, body condition (bc) and by-catch.

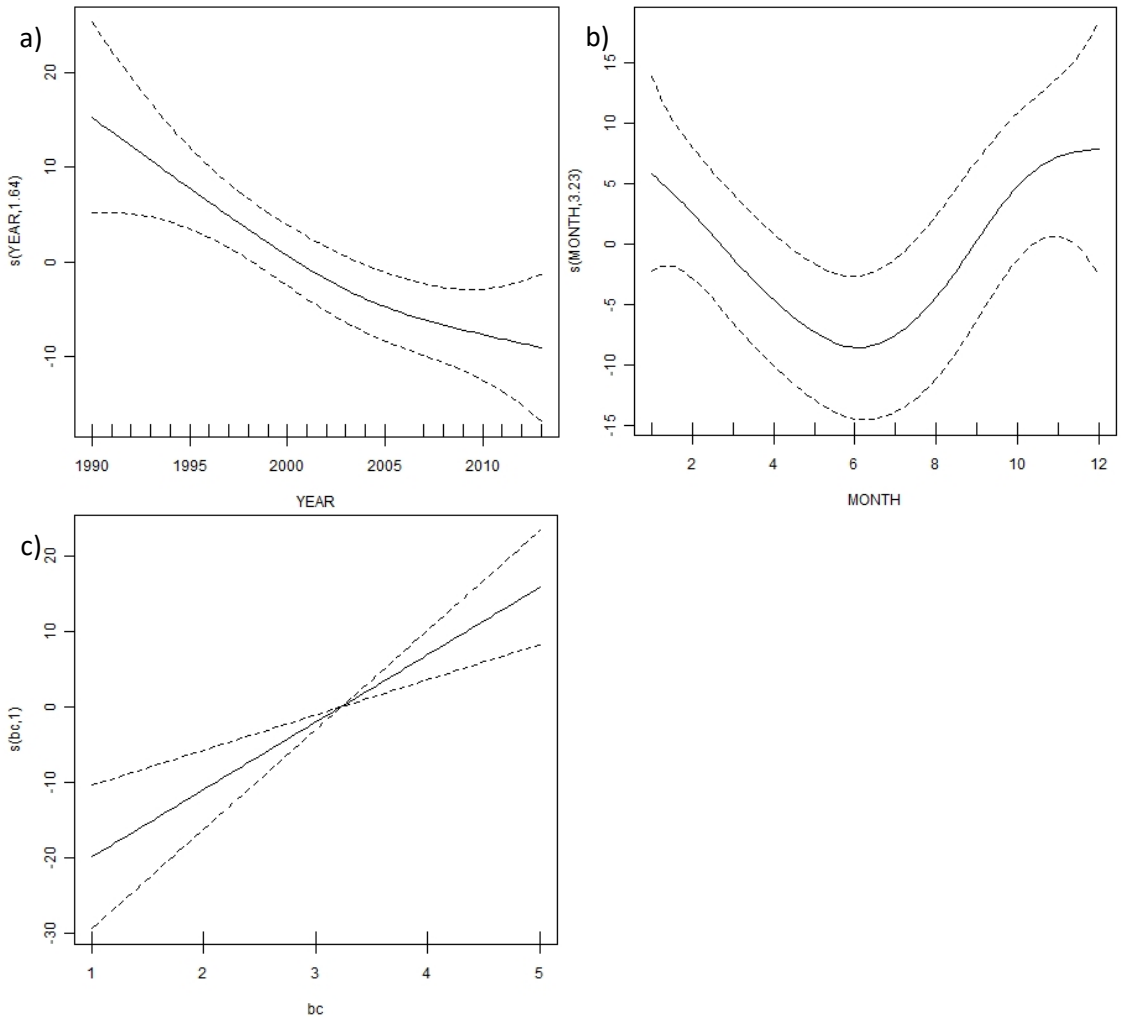


Figure 52. Graphs of the significant covariates of the GAM fitted for Galicia to model the length of stranded porpoises (bc, body condition). Model Y5. a) Covariate year, b) covariate month, c) covariate body condition.

The percentages of males and females in the whole area were the same (44.79% each) and 10.42% of animals were of undetermined sex. In addition, for 5 animals the sex was not available and 45 individuals were of body condition 5. In Portugal, fewer females (43.37%) than males (45.18%) were found (11.45% without sex determined).

The same covariates as used in Galicia were fitted using a GAM to model the length of the porpoises stranded in the study area (Table 18 Model Y12; Fig. 53). Males were significantly smaller than females (mean length for females: 150.24 cm (S.D. 28.05), males: 144.28 cm (S.D. 21.53) in North Portugal; mean length for females: 151.74 cm (S.D. 27.61), males: 147.28 cm (S.D. 23.74) in the total area. The effect of by-catch on the length of the animals stranded was not significant. Smaller animals stranded in May and June, and larger animals were found in

subareas of the South of the study area. As for Galicia alone, porpoises found in worse body condition were larger than animals found fresh.

The effect of year, month, SA and by-catch on sex was also modelled (Table 3 Model Y13), but significant effects were not found for any of them.

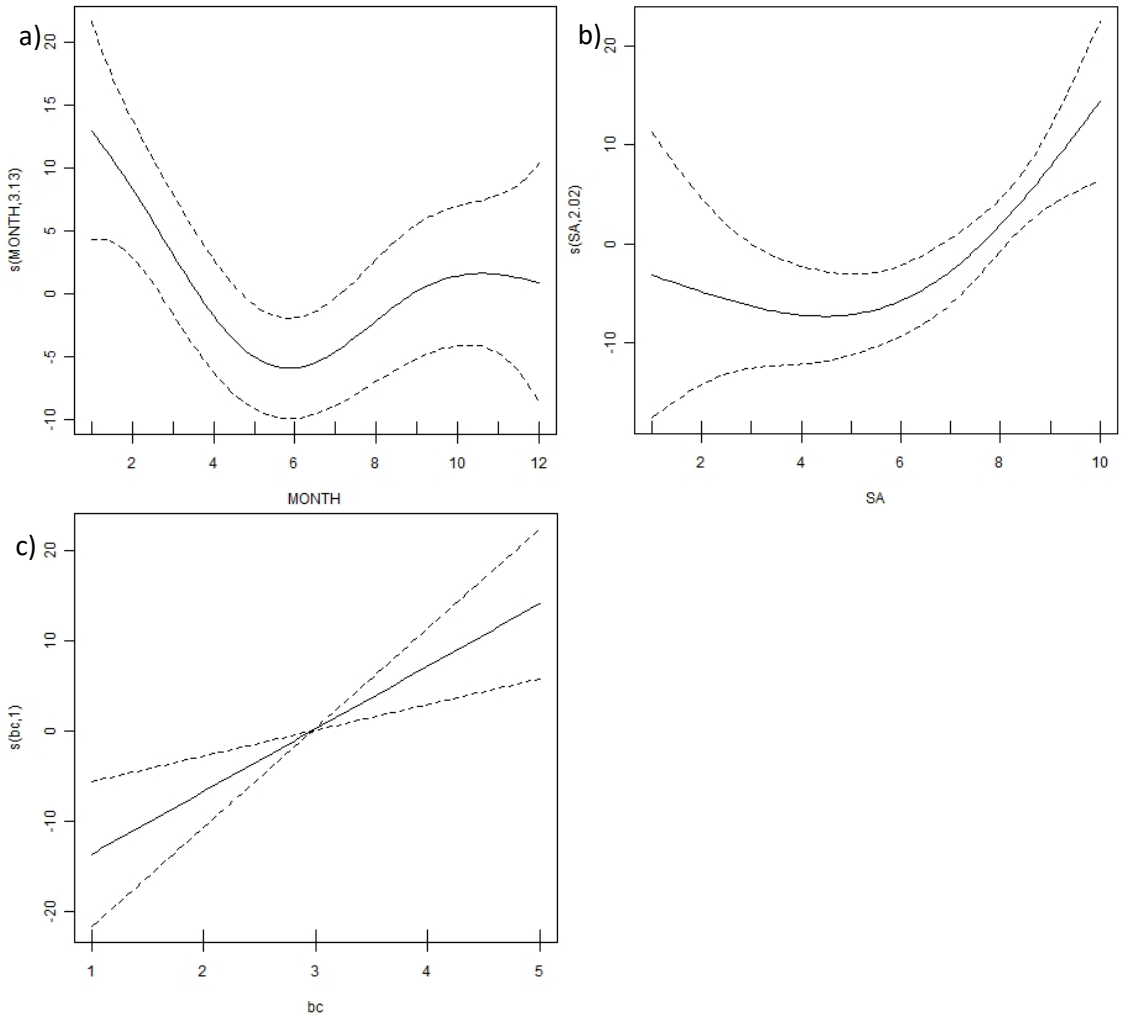


Figure 53. Graphs of the significant covariates of the GAM fitted for Galicia and North Portugal to model the sex of stranded porpoises (bc, body condition). Model Y12. a) Covariate year, b) covariate month, c) covariate body condition.

Trends in by-catch in Galicia from 1990 to 2013.

In Galicia, 26.24% of the porpoises stranded were classified as by-catch. When a GAM was fitted to study the effects of year, month, SA, length, sex and body condition, only the last one was found to be significant (Table 18 Model Y7, Fig. 54), and showed that most porpoises by-caught were found in body condition 2 or 3, which is not surprising as for animals in stage 4 and 5 it is impossible to detect by-catch signs. Therefore, bycaught animals tend to be more fresh.

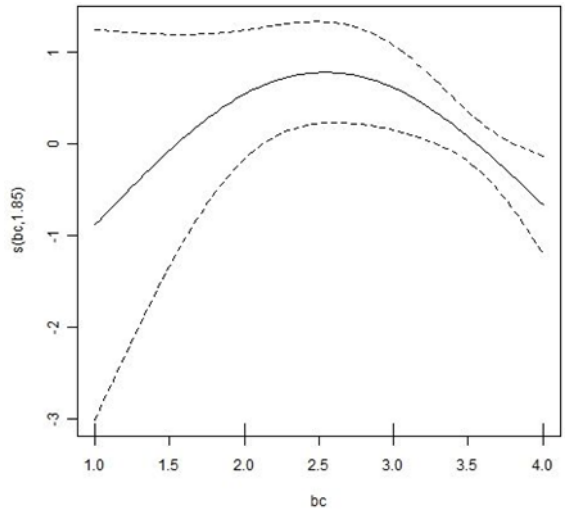


Figure 54. Graphs of the significant covariate, bc (body condition), of the GAM fitted for Galicia to model by-catch on porpoises strandings. Model Y7.

Trends in by-catch in Galicia and North Portugal from 2000 to 2013.

The percentage of animals found by-caught or with signs of by-catch in the study area was 33.42% and in Portugal 55.95%. In relation to the model fitted, only the covariates SA and body condition were significant (Table 18 Model Y14, Fig. 55). The number of by-caught porpoises had a positive trend from North to South. For body condition, similar results as for Galician data were found.

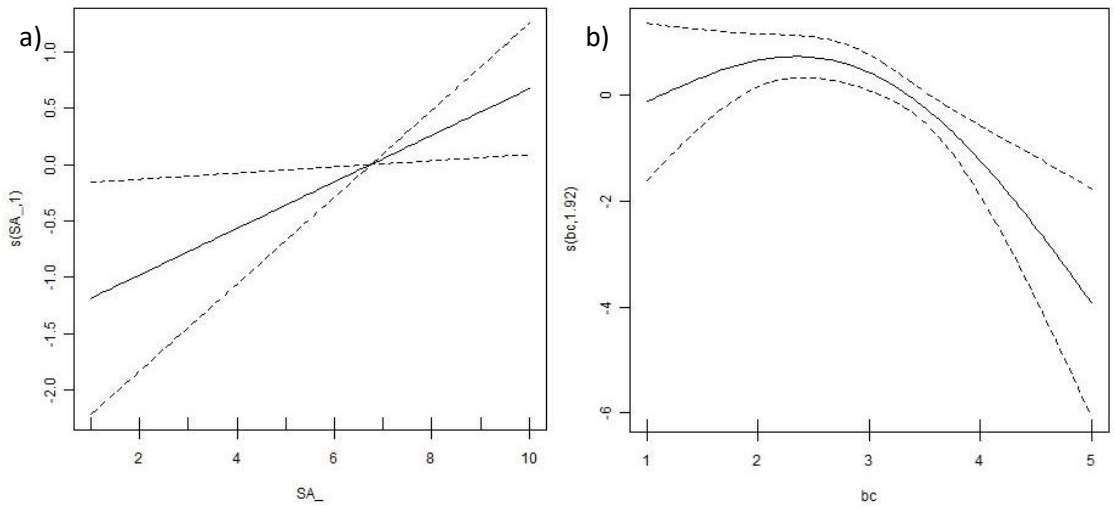


Figure 55. Graphs of the significant covariates of the GAM fitted for Galicia and Portugal to model by-catch on porpoises strandings. a) Covariate sub-area (SA), b) covariate bc (body condition).

Discussion

Strandings have been described as a good indicator of the species present in an area by several authors (Maldini et al 2005, MacLeod et al 2005, Pyeson 2010, 2011). Previous studies in Portugal and Galicia show that species of stranded cetaceans are comparable with species sighted (López et al 2002, 2004, 2012, Pierce et al 2010, Ferreira et al 2012, Santos et al 2012). Differences can be detected in the most sighted or stranded species. The presence of the coastal bottlenose dolphins means that the number of sightings of this species will be larger than for the most common species stranded in WIP, i.e. common dolphin (López et al 2002, 2004). Common dolphin strandings are followed by bottlenose dolphin (in Galicia) or harbour porpoise (in Portugal) (López et al 2002, Ferreira et al 2012). Besides, strandings report the presence of species that are not sighted easily and then can be detected, such as false killer whale (*Pseudorca crassidens*), pygmy sperm whale (*Kogia breviceps*) and blue whale (*Balaenoptera musculus*) (Penas-Patiño and Piñeiro 1989, López et al 2002, López 2003, Covelo et al 2009, Ferreira et al 2012).

The analysis of stranding data was carried out for Galicia and Portugal together, but also dividing the data in two groups: Galicia and Portugal. A total of 424 strandings of harbour porpoises were recorded in the whole study area (57.31% in Galicia and 42.69% in Portugal). Differences between years were found, and an increase in the number of strandings with time was detected, as was found in other areas of Europe (Jepson et al 2005, Leeney et al 2008, Pikesley et al 2011, Peltier et al 2013). The highest number of porpoises stranded was recorded in 2011 and the lowest was recorded in 2001, but it has to be kept in mind the difference of the range of years of each pool of data: Galicia from 1990 to 2012, Portugal from 2000 to 2012. In Galicia the highest number of strandings was recorded in 1998, in Portugal it was in 2011. In Portugal, the peak in 2011 was also found in strandings by Ferreira et al (2012), but in the current study, which analysed more years of data, it was also found that 2013 had a high number of strandings.

In some areas of Europe, seasonal variation was seen in the number of strandings. For example, around the North coast of Anglesey (Wales, UK) porpoise sightings increase in summer and decline in winter months (Shucksmith et al 2008), in Cardigan Bay, somewhat further south in Wales, porpoises were more abundant in winter (Simon et al 2010). Although those differences could be due to the presence of *T. truncatus* in Cardigan Bay.

Pikesley et al (2011) found a correlation between sightings and strandings of porpoises in Cornwall and South-west Britain and monthly patterns with peaks in winter. Leeney et al (2008) suggested that seasonal trends in strandings in the waters around Cornwall were related to changes in cetacean distribution and abundance, as well as in levels of fisheries by-catch. Jepson et al (2005) described a seasonal difference in the distribution of harbour porpoise strandings between Wales and south-east England, data suggested a possible north-south seasonal migration, and stranded harbour porpoise bycatches were most frequently recorded in south-west England comprising 40% of the total number of UK-stranded harbour porpoises diagnosed as bycatch. Jauniaux et al (2002) also found seasonal variation with the majority of strandings occurring during winter and early spring in Belgium and Northern France, and in the German North Sea Gilles et al (2009) detected a seasonal distribution of the species with important aggregation zones in offshore waters, a strong north-south density gradient in summer and a more even distribution in autumn. It would be expected that such seasonal variation in sightings would lead to a variation in the number of strandings. Siebert et al (2006) found that most strandings of porpoises along the shores of the German North Sea coast were from June to August, the same period when there was the highest number of incidental sightings of that species. Also, there was a strong seasonality of sightings in the German Baltic Sea, which were confirmed by aerial-surveys.

The results of the current study showed that harbour porpoise strandings occur throughout the year as previous studies in Portugal and Galician coasts suggested, and that here there were also differences between months. Moreover, the difference between months were different between both areas, whereas in Galicia the peak of porpoise strandings were on March and May, in Portugal that peak was later in the year, in May and June (Fig. 45). In Galicia porpoise strandings were more common in winter with a peak in March (López et al 2002), which agrees with current study that also found other peak in April. In Portugal Sequeira (1996) found that strandings in 19th century and until December of 1994 are more numerous in winter and spring. More recent study with data from January 2000 to December 2005 (Ferreira 2007) showed a small peak in May and June, but without significant differences between months. In the present study, the peak in May was also detected but not the other one. When all strandings data are pooled together (Galicia and Portugal data of present study), the number of strandings is higher in winter than in summer. The analysis of land-based data (Chapter IV, Pierce et al 2010) did not find clear seasonal trends in the number of sightings, while results from boat-based surveys (Chapter III) showed higher number of detections in June and October.

Together with the temporal variation of the number of strandings, it is interesting to analyse the distribution along the coast of the study area. In the WIP, there is an increase in the number of porpoises stranded from North to South with two regions showing particularly high numbers of strandings: SA.5 and SA.9 (Fig. 56). In Galicia, López et al (2002) detected an irregular distribution of the strandings with 97% of the strandings concentrated in SA.5 and SA.6, in contrast, if the result is compared with sightings from land-based surveys, it is found that the SA.5 is the one with no sightings (Chapter IV, Pierce et al 2010). On the other hand, in Portugal if results are compared with boat-based surveys the area with most strandings is also the one with most sightings (Santos et al 2012), and agrees with the results of Sequeira (1996) that describes a regular pattern of the strandings, with 96.25% of them recorded along the northern and central zones.

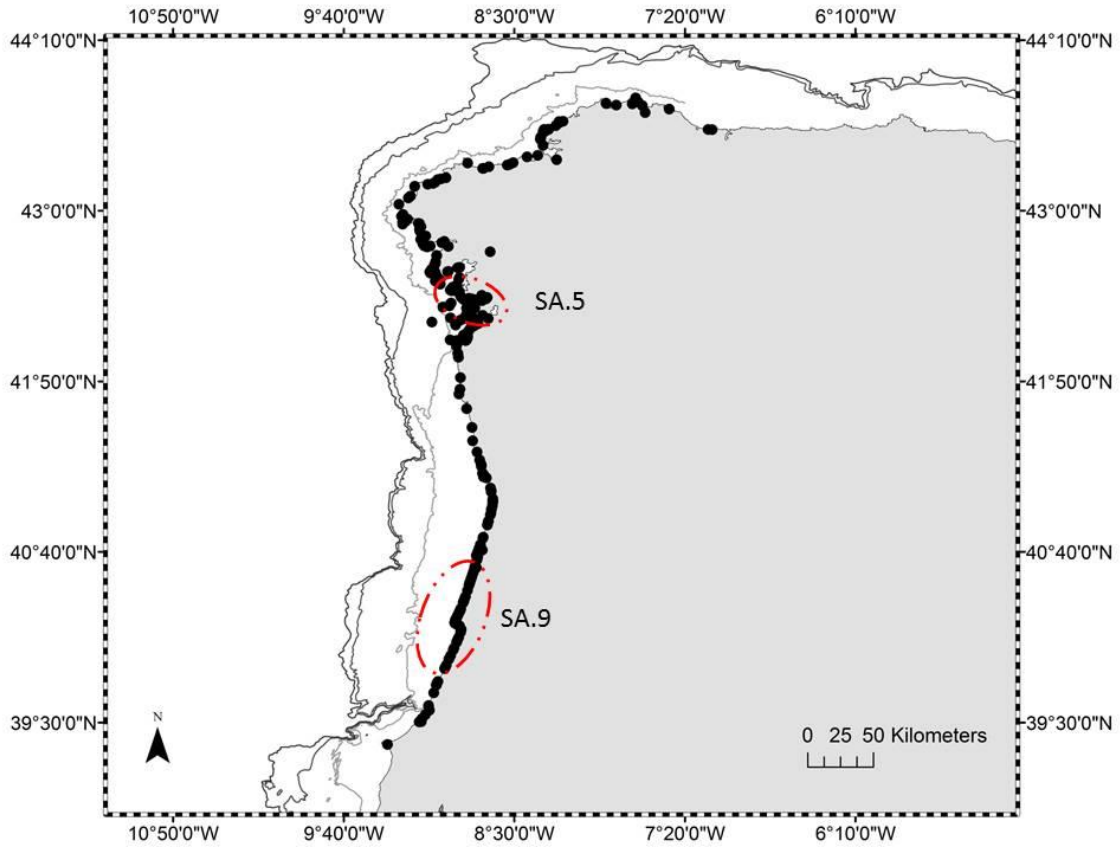


Figure 56. Areas showing particularly high numbers of strandings: SA. 5 and SA. 9.

Therefore, although it is expected that areas with highest occurrence of sightings will be also the ones with highest number of strandings, here, and especially in Galicia, there may be other factors influencing the presence of carcasses in the coast, e.g. seasonal current.

Because of oceanographic features such as currents, tides, winds, sea-pressure gradients, bottom topography (Evans et al 2005, Leeney et al 2008, de Boer et al 2012, Peltier et al 2012, 2013), decomposition of the carcasses by scavengers (Peltier et al 2012) or the sinking of the body, not all the dead animals arrive on the shore or they do so but in different areas from where they were living. There are several studies that tried to find out the proportion of cetacean deaths in the sea that result in strandings. Martinez-Cedeira et al (2011) worked with fishermen who tagged 23 by-caught dolphins and released them again into the sea. Of them, 5 reached the shore and were found travelling distances between 27 and 320 km. De Boer et al (2012) tagged 4 animals in Southwest England, but none was recovered. Finally, Peltier et al (2012) tagged 100 animals in the French Atlantic but only 8 were found on the coast. They also studied how wind and tide affect the drifting of carcasses, to explain where they strand and where they come from. Conclusions include the fact that the number of animals that strand is a small fraction of the ones that die in the continental shelf, but they allow to assess mortality both numerically and spatially, relative abundance, species richness and distribution of cetaceans.

In the West Iberian Peninsula (WIP), winds from North are predominant in summer and winds from South predominate in winter (Cabanas 1999). The orientation of the coast can have some impact in the difference of the number of strandings between areas. Coastlines oriented to the North are less influenced by winds from South and Southwest that are predominant in winter, than coastlines oriented to the West. The influence of the tidal current begin over the continental shelf around the 100 m isobaths, increases closer to the coastline, and is most evident at the mouth of the rías and in some narrow areas between isles and the tidal range is of around 3 m (Cabanas 1999). And, also on coastlines with more sandy beaches, carcasses may remain for longer periods of time than in steep rocky areas.

Other important factors that may affect to the behaviour of the carcasses in the sea are currents. In the WIP there is the Portuguese Current, a broad equatorward current and a branch of the Northward Iberian Poleward Current (IPC), called the Navidad Current (Pingree and Le Cann 1989), which enters the Cantabrian Sea.

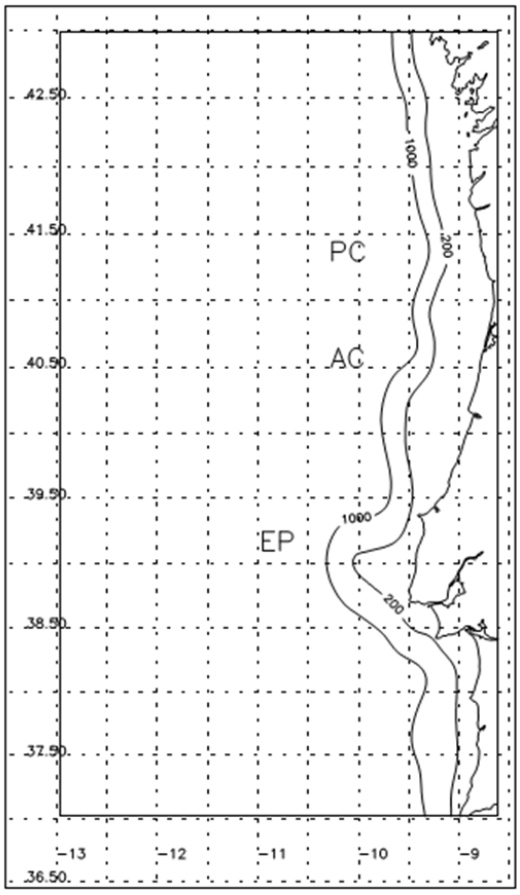


Figure 57. Domain of computation (inside the solid thick line) and topography (isobaths 1000 m and 200 m). The labels represent the main topographic features: EP, Estremadura Promontory; PC, Porto Canyon; and AC, Aveiro Canyon (from Peliz et al 2003).

In addition, the upwelling system present along the Galician and Portuguese coast is a relevant factor. It is the northern limit of the NW African upwelling system and is seasonal, caused by northerly winds during summer and Eckman transport (e.g. Fraga 1981, Prego and Varela 1998, Figueiras et al 2002). It is associated with the IPC (Álvarez et al 2003), and the interaction of coastal upwelling and strong outflow from the rías generates eddies in the slope with poleward flow. Eddies can be generated also by topographic features as happens in the Estremadura Promontory, the Aveiro Canyon and the Porto Canyon (Fig. 57, Peliz et al 2003). Those eddies could contribute to breakdown of the Iberian Polar Current (IPC) during the start of the upwelling regime (Torres and Barton 2007).

Following the results of Sala et al (2013) carcasses of cetaceans dead at sea in the North West Peninsula will travel toward the east could reach the Cantabrian Sea due to the Navidad Current; on the other hand, carcasses in the rest of the West Peninsula coast will drift southwards probably due to the IPC.

Finally, storms are more frequent during autumn and winter and can influence strandings, both by carrying carcasses towards the coast due to southern winds and by causing the death of animals in poor condition (López et al 2002).

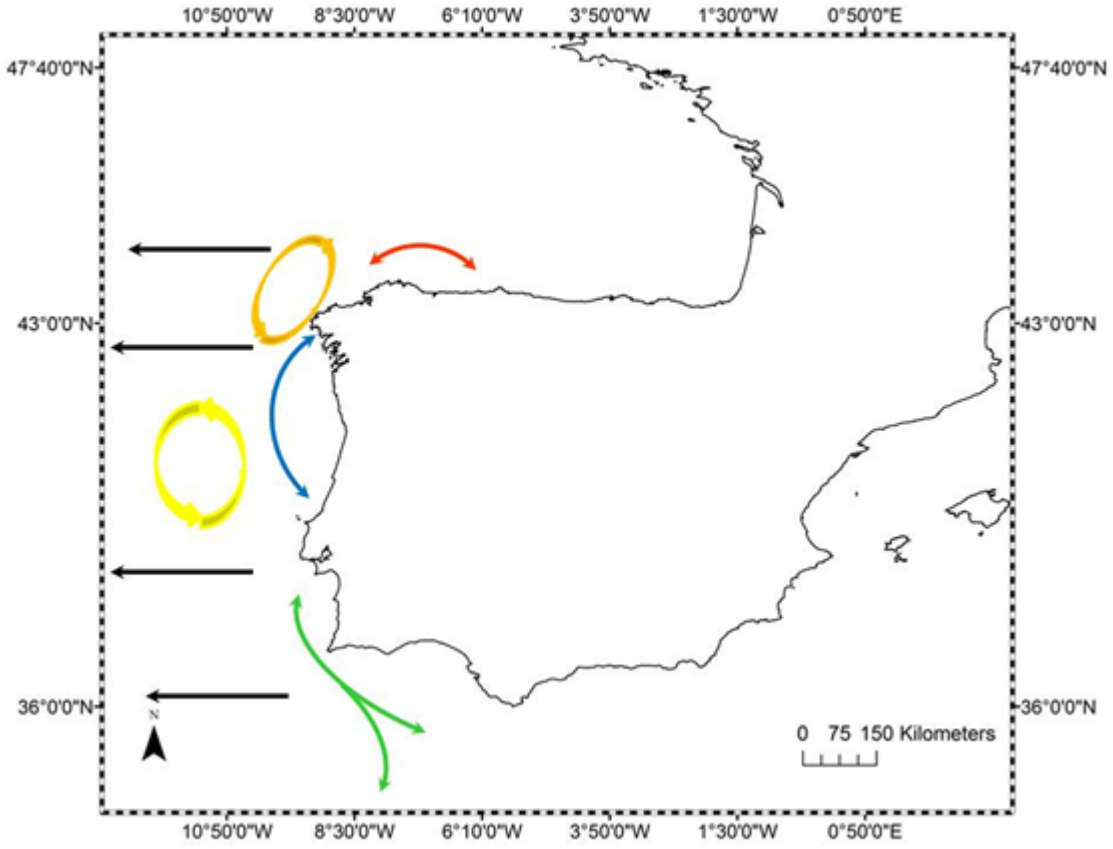


Figure 58. The possible movements of cetacean carcasses stranding on the Iberian Peninsula coasts are: i) remain or be driven to offshore waters (black arrows) ii) be driven to Asturias and Galicia (red arrows), iii) to different areas of Galicia (orange arrows), iv) to Galicia and Portugal (blue arrows), v) to different areas of Portugal (yellow arrows), vi) to Portugal and Gulf of Cádiz, Gibraltar Strait or even North Africa (green arrows).

Then, there is the possibility of cetacean carcasses stranding in different areas from where they live. In the study area there could be a "mixture" of carcasses originating from i) Asturias and Galicia, ii) different areas of Galicia, iii) Galicia and Portugal, iv) different areas of Portugal, and perhaps less plausibly, v) Gulf of Cádiz, Gibraltar Strait or even North Africa (Fig. 58).

The oceanographic features present in the WIP coast and the situation of the WIP itself, reduce the probability of carcasses belonging to other areas reaching this coast. This is especially important in the case of harbour porpoises, the Iberian population of which has been described to be isolated from the rest of porpoises of the European waters and does not

show any population structure along the Spanish and Portuguese coasts (Fontaine et al 2007, 2010, 2014, Alfonsi et al 2012, Chapter II).

The probability of stranding is not the only important issue, the probability of finding the carcasses is important as well. Variation in the observation effort of the Stranding Networks can lead to temporal trends that do not reflect the distribution, abundance or mortality of the animals. Also, the increase of human habitation, coastal activities, presence of people in the beaches in summer and proportion of beaches in the coast line can have an effect. Since 1999 in Galicia and 2000 in Portugal, the effort of strandings networks has stabilized, but in last years there may had been an ongoing increase of stranding reports by people present on the beaches due to the ease of access to the authorities.

It is estimated that in Galicia up to the 25% of the animals that die in the sea reach the shore (Martinez-Cedeira et al 2011). Peltier et al (2012) estimated that, under the assumption that all dead carcasses float and drift, the probability that a stranded cetacean is discovered is only of 12.9%. Therefore, a rather small proportion of dead animals are likely to be recorded and necropsied, but they can still provide relevant information on mortality at sea, relative abundance, species richness and distribution of cetaceans (Maldini et al 2005, MacLeod et al 2005, Pyeson 2010, 2011, Peltier et al 2012), and in this case about the Iberian harbour porpoise population.

Together with the information on presence/absence and spatiotemporal trends, strandings provide data about life history, diet, health, contaminants, genetics or cause of death (e.g. Siebert et al 1999, Jauniaux et al 2002, Santos and Pierce 2003, Das et al 2004 a, b, Santos et al 2004, 2005, Murphy et al 2010, Lopez et al 2012, Read et al 2012, Stocking et al 2013, Fontaine et al 2014, Méndez-Fernández et al 2014 a, b). In this study the sex, body length and by-catch were analysed.

In the WIP there was the same proportion of males as females (44.79% each), although the number of females was slightly lower in Portugal. The total body length ranged from 81 to 202 cm with a mean length of 146.66 cm, the Portuguese porpoises being larger than Galician, and females larger than males. These sizes agree with previous studies that described the Iberian porpoises as larger animals than those of other areas (e.g. Donovan and Bjørge 1995, Sequeira 1996, Lockyer 2003, Lopez 2003, Read et al 2012, Lopez et al 2012). The larger animals stranded in winter and carcasses were fresher when animals were smaller. This could be due to the presence of larger animals close to the coast in winter and then they strand more. Also,

the smaller porpoises strand fresher as they are close to the coast and they get the shore sooner than those in farther areas.

Finally, the presence of by-catch evidences (absence of tail/flippers, presence of ropes, net marks) was also analysed. By-catch is one of the principal threats for small cetaceans, especially harbour porpoises (IWC 1994). In an area of high fishing effort such as WIP (Sequeira et al 1992, EUROSTAT 2010) interactions between fisheries and cetaceans has become aspect topic of great concern in recent years that has lead to the development of projects such as LIFE-INDEMARES and DIVULGANDO A PÉ DE MAR in Galicia and SAFESEA and LIFE MarPro in Portugal, as well as a number of publications on the topics (e.g. Lopez et al 2002, Fernández-Contreras et al 2010, Ferreira et al 2012, López et al 2012, Read et al 2012, Goetz et al 2014). Relatively few cetacean by-catches are directly reported by fishermen, so this problem has to be studied with observers on board fishing boats, interviews or by diagnosis during the necropsies. In Galicia, the majority of the by-catches are common dolphins (23%), but other species such as harbour porpoises (22%) and bottlenose dolphins (14%) are also by-caught (López et al 2002, 2003). In the current study, it was found that on average 33.42% of the stranded porpoises had signs of by-catch with a higher proportion in the Portuguese coast (55.95%) than in the Galician (26.24%). That difference was also highlighted by Read et al (2012) who suggested that one of the reasons could be that gillnets are one of the gears that cause the highest rates of by-catch in Galicia whereas in Portugal, although gillnets are also problematic, the beach-seines are commonly used in North-Central Portugal and are thought to be one of the gears to which harbour porpoises are most vulnerable (Sequeira and Inácio 1992, López and Valeiras 1997, López et al 2003, Ferreira 2007). Ferreira et al (2012) suggested that in Portugal the interaction with fisheries is the cause of 44 - 54% of the registered cetacean deaths, including 58% for porpoises (Ferreira 2007).

Since the detection of signs of by-catch in carcasses depends on its state of decomposition and the amount of animals that reach the shore, the number of cetaceans that die due to interactions with fisheries is probably underestimated (although the proportion of mortalities that are due to bycatch may be accurately estimated). Despite that, the rates found suggest that the bycatch mortality is unsustainable, as suggested by Ferreira (2007), López et al (2012), Read et al (2012) and Goetz et al (2014) according to ASCOBANS (1997), which state that an anthropogenic removal of more than 1.7% of the best available population estimate abundance represents an '*unacceptable interaction*'.

This differentiated and isolated harbour porpoise population of the WIP faces an important problem, and as an area with a great socio-economic importance of fisheries, it is difficult to reduce and impossible to totally avoid by-catch. However, measures to reduce that problem and specific management plans for porpoises should be developed. Different measures can be developed in this area, such as i) the reduction of the use of gears that cause damage to porpoises or restriction of their use in areas where the species has high densities, ii) the use of acoustic deterrent devices ("pingers"), to alert porpoises of the presence to nets and iii) use of acoustic reflective nets, to reduce the likelihood of entanglement by modifying the behaviour of the animals and increment their ability to detect nets, which have been proved to be effective for porpoises in several areas (see Dawson et al 2013 for a review of the use of pingers, Trippel et al 2003, Larsen et al 2007), and can also reduce the economic cost of damage to nets and caught fish. However, it has to be kept in mind that such devices increase the noise in the sea and there is the possibility of causing the exclusion of the species from areas where they normally feed, or also can attract other cetacean species that are not afraid of acoustic signals or adapt them as bottlenose dolphins. Also there could be a reduction of the catch of the target species and ease of handling for fishermen of some modified nets (Trippel et al 2003, Larsen et al 2007, Dawson et al 2013, Goetz et al 2015).

CHAPTER VI

General Discussion

The present study aimed to improve the understanding of the status and ecology of the harbour porpoise, *Phocoena phocoena*, in the Iberian Peninsula. Genetic approaches were used to examine population substructure and generalised additive models were used to study the habitat preferences of porpoises in Galician waters, NW Spain. In addition, seasonal and spatiotemporal trends of porpoise strandings, and by-catch presence were studied. The main results of this study can contribute to the determination of its conservation status and the planning and implementation of management plans for Iberian harbour porpoises.

Population structure of the Iberian harbour porpoise

The effective definition of protected areas and development of management plans as conservation tools require an understanding of the distribution, abundance and population structure of a species. This is especially important as the effect of a studied threat in an area can be over- or underestimated and can be a difficult issue in cetaceans. These species are highly mobile and live in an environment which has non-obvious geographic barriers to gene flow. Different studies have identified habitat discontinuities and changes in oceanographic features as influencing the spatial genetic structure of several delphinid species (e.g. Hoelzel et al 1998, Fullard et al 2000, Natoli et al 2005, Bilgmann et al 2007, 2008, Möller et al 2007, 2011, Rosel et al 2009, Amaral et al 2012 a, b, Ansmann et al 2012, Gaspari et al 2013, Richards et al 2013). This may be the reason for the strong barriers to gene flow detected in porpoises in southern Bay of Biscay because of the warmer and deeper waters in that area which make this area unfavourable for porpoises (Fontaine et al 2007, Alfonsi et al 2012).

In the present study, there was a clear genetic separation between the Iberian Peninsula population and the rest of Northeast Atlantic and Black Sea, and a connection with the population of West Africa. Also it was found that there was no significant pattern of population genetic structure in harbour porpoises along the Iberian Peninsula coast. All these findings confirm the suggestion of the isolation of the Iberian population (Tolley and Rosel 2006 Fontaine et al 2007, 2010, Alfonsi et al 2012) which must be considered as one unique population and it is consistent with the assertion (Fontaine et al 2014) that they should be described as a separate subspecies, *Phocoena phocoena meridionalis.*

The recognition of this isolated population is essential for porpoise conservation and to assess threats that can affect them. Such small populations are at risk if they become fragmented and migration between those new subpopulations decreases or is eliminated, and then the rate of loss of genetic diversity can increase through inbreeding and strong genetic drift, which can

increase the probability of demographic, environmental and genetic stochasticity. This can negatively affect the long-term viability of population fragments and therefore of the entire population.

Frankham et al (2002), Frankham (2005) and Garner et al (2005) found that endangered species have lower genetic diversity than non-endangered equivalents, which increases their vulnerability and consequently increases probability of extinction (Mills and Smouse 1994, Lacy 1997, Frankham et al (2002), Frankham (2005). Then, it is of concern that porpoises in Spain and Portugal had similar nuclear and mitochondrial genetic diversity, which were lower than in all the other populations except those in the eastern Mediterranean.

Modelling the influence of different factors affecting the detection of harbour porpoises by observers in Galician waters

For the conservation of a species it is important also to know the environmental conditions and areas where it is present to preserve the species and avoid any anthropogenic action that would negatively affect its survival. Habitat modelling techniques represent a potentially powerful tool for predicting cetacean distributions and understanding the ecological processes determining these distributions. This approach has already been used to incorporate this environmental variability into management applications, including improvement of abundance estimates, development of marine protected areas, and understanding cetacean–fisheries interactions (Redfern et al 2006). The current study is focused on the harbour porpoises of Galician waters. The aim was to improve knowledge of the environmental conditions and areas in which porpoises were seen with higher probability so that suitable areas for their conservation can be established with more accuracy.

Cetacean data used in habitat modelling may come from both dedicated and opportunistic studies including ship, aerial, and acoustic surveys, as well as individual tagging studies (Redfern et al 2006). In this case, two sets of data were used: i) data recorded during targeted boat surveys carried out in Galician coastal waters during the years 2003 - 2010; and ii) data from land-based surveys carried out from a series of observation points along the coast to cover the study area as evenly as possible.

In the first place and to avoid a possible underestimation of the population or even an incorrect interpretation of lack of sightings as absence in an area, it is important to identify the factors that can have some influence on the detection of cetaceans by observers and that should be taken into account. This is especially important for harbour porpoises, which are

difficult to detect due to their small in size, cryptic surfacing behaviour (it is relatively rare to see more than the dorsal fin and a part of the back), doing long dives between breathing sequences, spending little time at the water's surface, and often solitary (Westgate et al 1995, Read 1999, Heide-Jørgensen 2013).

As many other authors found before (Palka 1996, Evans and Hammond 2004, Weir et al 2007, Tynan et al 2005, Marubini et al 2009, Embling et al 2010, Pierce et al 2010, Booth et al 2013, Dolman et al 2013, de Boer et al 2014,) analysis of data collected by both methods (boat and land-based surveys) identified sea state to have an important influence into the probability of detection of porpoises, decreasing as Douglas and/or Beaufort increases. Also, the probability of detecting harbour porpoises increases with the area available for survey (i.e. the field of view), but in boat-based surveys there is a distance from the boat at which this trend is no longer seen and in land-based surveys there is a size of the area above which the observers will probably not scan all the area with the same effectiveness.

The boat-based survey data also showed that the best boat speed for monitoring harbour porpoises is around 6 knots, in contrast to other studies in which this variable was the only survey variable studied that did not have an effect on the sighting rates (Booth et at 2013) or was important but only for one year of study with a decrease of the detection rate for boat speed higher than 6 knots (Embling et al 2010). Lower or faster speeds could decrease the probability of detecting porpoises. They can more easily avoid a slow travelling boat (Culik 2004, personal observation). And at high speeds porpoises are less likely to be detected as they spend short time at the surface and cannot easily be seen if they are diving while the boat passes through the area where they are. At slow speeds another issue might be that slow porpoise sightings are duplicated as individuals could be detected several times as the boat passes.

On the other hand, analysis of land-based survey data showed that time of observation was an important variable affecting the observers. It was found that the longer the time period of observation, the higher probability of detecting porpoises. Because the observers can get tired, there also should be a maximum duration of the observation period to avoid a decrease in the efficiency of the search, which in the current study begins approximately at 100 minutes (although it is also difficult to be precise about this as relatively few observations lasted longer than 100 minutes). Moreover, it was found that the presence of bottlenose dolphins has an important influence on the probability of detection of porpoises in Galician waters. There can be different reasons for this effect, for example the possible avoidance by porpoises of

competition and/or attacks (López and Rodríguez 1995, Alonso et al 2000, Mendez-Fernández et al 2013) or the distraction of observers from seeing porpoises due to the presence of bottlenose dolphins (*Tursiops truncatus*). However, it is important to note that an apparently negative relationship could arise simply due to the two species having different habitat preferences.

Habitat preferences of harbour porpoises from Galician waters

As was said before, for conservation purposes habitat modelling techniques are used frequently to predict cetacean distributions and understand the ecological processes that determine those distributions (Redfern et al 2006).

In the present study, several environmental covariates were found to be important for the presence of harbour porpoises in Galician waters. Analysis of data collected by both methods found that the depth of the eutrophic zone (ZEU) was significant in the models fitted, with an increase in porpoise presence as values of that variable increased. This zone is the depth range where the Photosynthetically Active Radiation (PAR) is sufficient to support photosynthesis (Kirk 2011). Thus, the highest values of ZEU indicate areas of high productivity (Haande et al 2011, Jin et al 2011, Khanna et al 2009). Another important variable found, in this case in boat-based surveys, was chlorophyll concentration. High chlorophyll conditions again signify high productivity and can be related with the upwelling conditions that are usual in the study area (e.g. Fraga 1981, Figueiras et al 2002, Álvarez et al 2005, 2010, 2012). Upwelling conditions have been described as one of the most important variables influencing the presence of porpoises in California (Tynan et al 2005), Eastern North Sea (Skov and Thompsen 2008) and the German Bight (Gilles et al 2011).

Previous work in the same area has provided contradictory results, although based on different methodology. Fernández et al (2013) found that porpoises sighted at sea were present at a wider range of CHL_a concentrations than other species during summer. A previous analysis of the first four years of coastal sightings data found that porpoises were seen most frequently adjacent to the coast in less productive areas (Pierce et al 2010) which was suggested to be a consequence of preferred water temperature and depth of the species and possibly of avoiding bottlenose dolphins (which were found in the most productive coastal areas). However, it should be noted that productivity was examined at a fairly coarse spatial scale, based on data from several transects along the coast.

In the present study, the positive relationship found is consistent with studies in other areas such as California (Tynan et al 2005), Bay of Fundy (Johnston et al 2005) and the North Sea (Gilles et al 2011). Thus the results of the present study also suggest that porpoises were mostly detected in more productive areas. The increase of nutrients in the water due to the upwelling of nutrient-rich waters leads to an increase in primary productivity and therefore the chlorophyll concentration, and later to the secondary productivity which will lead a higher presence of porpoise prey in the area. However, as suggested by the apparently contradictory results mentioned above, it is also important to consider the spatial scale most relevant to porpoises. It would be expected that porpoises favour areas of high prey density and/or conditions in which high prey densities normally occur, but it is not obvious for example whether porpoises would be most sensitive to variations at a scale of a few metres, hundreds of metres or several kilometres.

In land-based surveys, Easterly winds also appeared to be an important factor for the presence of porpoises, with an increase of porpoise detections when there were Easterly winds. Those winds can also create conditions of upwelling Galician coast which will allow to deeper and richer waters to emerge, increasing the productivity of the area, also in areas far from the coast (Torres et al 2003).

On the other hand, during boat-based surveys porpoises were mostly seen in waters with medium temperatures (between 16 – 18°C), a normal situation during summer in Galicia (Fraga 1981, Triñanes et al 1993, www.meteogalicia.es) when the Eastern North Atlantic Central Water (ENACW), a salty subtropical water mass is upwelled. However, porpoises are often described to be mainly present in colder waters (e.g. between 5 - 14°C; Evans and Teilmann 2009). The importance for the Iberian harbour porpoises of the temperature found here suggests that they are sensitive to temperature variation. This could be due to the effect of temperature on porpoises itself, on porpoises prey or even just an effect due to the higher number of surveys or the best conditions to detect porpoises during that season. For the first reasons, an increase in water temperature, due to climate change, for example, in this area may be of concern as it is near the southern limit of harbour porpoise distribution, and perhaps close to its thermal limits (e.g MacLeod et al 2005, Learmonth et al 2006, Laidre et al 2008, MacLeod 2009, Lambert et al 2011, 2014).

Other environmental covariates that were found to be important for porpoises in the study area were related with seabed slope. Seabed slope has been found to influence porpoise distribution in several previous studies (Embling et al 2010, Isojunno et al 2012, Booth et al

2013). In boat-based surveys there were more sightings where seabed slope is facing to the South. This could be due to the presence of a slope current which is stronger and more persistent than shelf currents and has an onslope tendency in mid depths (Pingee and Le Cann 1989). In the study area, this current is known as the Iberian Poleward Current (IPC) (Peliz et al 2003) and the Portugal Coastal Counter Current (PCCC) (Ambar and Fiúza 1994). Often this poleward undercurrent causes the appearance of upwelling water, as happens in Galicia. Moreover, in the areas where slope faces south, this current can increase, becoming stronger at a local scale. For example, in the Horns Reef area (eastern North Sea), upwelling was described as the most important habitat characteristic for the distribution of porpoises that alternate between two upwelling cells depending on the direction of the tidal currents (Skov and Thompsen 2008). Also, in the German Bight, porpoises preferred areas with stronger currents and concentrated in areas where fronts are likely (Gilles et al 2011). Several studies found that porpoises were related with different sorts of currents, including tidal currents, although they are normally at a small spatial scale.

From land-based surveys data, it was found that more porpoises were detected in waters where sea bed slope was greater, depth was more variable and the continental shelf was narrower. These will be areas where deep waters occur close to the coast, highlighting the importance of the areas where the shelf is narrower, which was also found by Pierce et al (2010), who argued that this could indicate that porpoises habitually occupy deep waters in Galicia. Since then, several studies confirmed this, showing that in this area porpoises are seen in waters with depths between 50 - 100 m, with several detections in 100 - 200 m (Spyrakos et al 2011, Fernández et al 2013). The importance of depth for harbour porpoises is clear, but the relationships are different depending on the area (Read and Westgate 1997, Carretta et al 2001, Bailey and Thompson 2009, Marubini et al 2009), thus it seems that preferred depths are a consequence of local conditions rather than being a consistent characteristic of porpoise habitat choice.

Effects of both upwelling conditions and depth on porpoise presence could be related with the diet of harbour porpoises in Galician waters. Upwelling and primary productivity are linked to higher trophic levels through the food chain. Highly productive areas of upwelling or eddies may be good for the development and aggregation of the most important prey of harbour porpoises in Galicia such as blue whiting, *Trisopterus* spp, silvery pout (*Gadiculus argenteus*) and *Trachurus* sp. (Pierce et al 2010, Read et al 2012) that can be found on the continental

slope (blue whiting) and in shelf waters (the other species), mostly in deep waters (Cohen et al 1990, Svetovidov 1986, Collete and Parin 1986, Smith-Vaniz 1986).

Other prey species dominate the diet of porpoises in other areas. In Scotland the main prey are sandeels (Ammodytidae) and whiting (Santos et al 2004), and in the Gulf of Maine it is herring (*Clupea harengus*) (Gannon et al 1998), which are found in waters of less than 200 m depth and generally are not present in Galician waters (Whitehead 1985, Muus and Nielsen 1999, ICES 2012).

Porpoise distribution is likely to reflect foraging opportunities, because by remaining close to food resources, porpoises may be able to more easily meet the energetic demands of maintenance, growth and reproduction. This is especially important in the case of mature females which have the additional costs of pregnancy and lactation that increase the energy requirements and often happen at the same time (Brodie 1995, Kastelein et al 1997, Read et al 1997, Read and Westgate 1997, Koopman, 1998, Lockyer 2007, MacLeod et al 2007 a, b).

It might be expected that porpoise distribution varies with the distribution and abundance of the prey. If the year-to-year trends in abundance of blue whiting (ICES 2012) are compared with porpoise sightings, years with highest abundance of blue whiting were not related with years with lowest sightings, which would be expected if porpoises moved to deeper water to feed on blue whiting. Ideally the relationships between porpoise and prey distribution and abundance need to be examined at finer spatial and temporal scales.

The environmental conditions in which porpoises of Galician waters were seen with higher probability are now better known, increasing the knowledge of this species in the area. The modification of those key habitat conditions for porpoises may affect the presence and survival of porpoises, so this information is potentially useful for the development of conservation plans and also for the definition of SACs as is required by Habitats Directive. Although EU Member States have this obligation and harbour porpoises are designated as ”vulnerable” in Spain (Catálogo Nacional de Especies Amenazadas, Law 4/1989, 2000), none of the existing Galician SACs has been established specifically for harbour porpoises, although there is a debate about the usefulness of marine protected areas to highly mobile species such as porpoises.

Patterns in harbour porpoises sightings along the Galician coast

There was variation in the number of porpoise sightings with year and this differed between land- and boat-based observations, although it should be kept in mind that there was a difference in the survey period for the two methods, which may lead to differences in the results. Whereas boat-based surveys were carried out only through some months of the year (from March to October), land-based surveys were carried out all year round. Also there is obviously a difference in the area surveyed, i.e. in relation to depth and proximity to the coast, so in some years porpoises could be closer to the coast and hence detected better with coast surveys than boat surveys, and *vice versa*. In addition, given the focus on the South coast of Galicia for the boat-based surveys, if porpoises moved North to northern in some years they would not be detected.

Boat-based surveys showed a significant increase in the number of sightings in 2005 and no detections in 2006 while land-based surveys showed an increase in the number of sightings over the years, at least during the last 5 years of surveys, with the year with most sightings being 2011 and the year with fewest records being 2007 (except for the three months of survey in 2003 when no porpoises were detected). Pierce et al (2010) also showed interannual variation in the number of porpoise sightings from land-based observations in the same area during 2003 - 2007.

In Galicia the apparent changes in porpoise distribution over the years could be due to: i) the use of different areas during the study period due to changes in prey distribution, abundance, movement from deeper to coastal waters; ii) the porpoise population is increasing, although the possible rate of increase of the population calculated from life history data (Read et al 2012) seems to be lower than the apparent increase seen in the present study (see Chapter IV); or, iii) the movement of individuals from other areas such as Asturias or Portugal, or from distant deeper waters to Galicia, but there are insufficient data at present to evaluate this possibility. Variation between years was also found in other areas of Europe, such as Scotland (Marubini et al 2009, Booth et al 2013) and the Baltic Sea (Benke et al 2014).

In addition, a temporal trend during the day was found in the land-based study. The number of sightings increased in later in the day, as indeed was found before by Pierce et al (2010). The reason why more sightings were recorded later in the day is not clear. It could be due to boat traffic especially in summer when there is a great number of pleasure boats active during the

day and boat traffic tends to decrease after 19.00 h (Pers. Obs.), thus noise decrease too. However, this needs further study.

There was also a spatial trend in the number of sightings from land, with more detections in Lugo and A Coruña (Northern stations), which is again broadly consistent with previous analysis of 2003 - 2007 data (Pierce et al 2010), which found that the sightings were more frequent around Punta Roncadoira (between observation points 2 and 3 in this work), and Cabo Vilán (observation point 13). In contrast, the peak found in that study in A Guardia (observation point 30, adjacent to the border with Portugal) was not detected here. As it was said before, this decrease in the number of sightings in the south of the study area could be due to changes in porpoises distribution or movements to other areas. It seems that Galician porpoises prefer areas with fewer and smaller rias, and avoid bigger rias such as the Rías of A Coruña, Pontevedra and Vigo, where bottlenose dolphins, apparently one of the most important factors affecting porpoise presence, are detected most frequently - and which are also highly industrialized areas.

Patterns in the strandings of harbour porpoises

Strandings are a good indicator of the species present in the area, as shown in Portugal, Galicia and many other areas (López et al 2002, 2004, 2012, Maldini et al 2005, MacLeod et al 2005, Pierce et al 2010, Pyeson 2010, 2011, Ferreira et al 2012, Santos et al 2012), although the proportion of each species from strandings and sightings is likely to be different, related to the distribution and abundance of the species and to the distribution of the main causes of mortality. Thus, coastal species will be most sighted from land-based and coastal waters surveys, i.e. bottlenose dolphins in Galicia and Portugal. However, the most commonly stranded species in West Iberian Peninsula (WIP) is the common dolphin (*Delphinus delphis*) followed by bottlenose dolphin (in Galicia) or harbour porpoise (in Portugal) (López et al 2002, 2004, Ferreira et al 2012), which is probably related to high numbers of fishery by-catch mortalities in common dolphins.

Strandings can also reveal the presence of species that are not sighted easily, such as false killer whale (*Pseudorca crassidens*), pygmy sperm whale (*Kogia breviceps*), blue whale (*Balaenoptera musculus*) or several beaked whales (Penas-Patiño and Piñeiro 1989, López et al 2002, 2003, 2004, López 2003, Covelo et al 2009, 2015, Pierce et al 2010, Spyrakos et al 2011, Ferreira et al 2012, Santos et al 2012, Fernandez et al 2013).

The analysis of stranding data was carried out for the whole study area, but also dividing the data in two groups: Galicia and Portugal. A total of 424 strandings of harbour porpoises were recorded in the whole study area (57% in Galicia and 42% in Portugal).

Differences between years were found. The highest number of porpoises stranded was recorded in 2011 and the lowest was recorded in 2001. If the areas are split, the minimum in Galicia changes to 1998. In Portugal, the peak in 2011 was also found in strandings by Ferreira et al (2012), but in the current study, which analysed more years of data, it was also found that 2013 had a high number of strandings. Overall there was no significant upward trend in the number of strandings over the study period, in contrast to what has been found in other areas of Europe where the number of strandings are generally increasing (Jepson et al 2005, Leeney et al 2008, Pikesley et al 2011, Peltier et al 2013).

Harbour porpoise strandings in Galicia and Portugal occur throughout the year as previous studies suggested, although there were differences between months, with the number of strandings higher in winter than in summer. Previous studies in Galicia found that porpoise strandings were most common in winter, with a peak in March (Lens 1997, López et al 2002). This peak was also found in the current study as well as another peak in April. In Portugal, Sequeira (1996) found that strandings from 19th century and until December of 1994 were more numerous in winter and spring. Ferreira (2007), with data from January 2000 to December 2005, found no significant differences between months. In the present study, a peak in May was detected in Portuguese porpoise strandings. Trends in strandings have been related with known changes in cetacean distribution and abundance, sometimes related with seasonal migration (Jepson et al 2005, Leeney et al 2008), or levels of fisheries by-catch (Jauniaux et al 2002, Jepson et al 2005, Leeney et al 2008), and as an indirect result of trends in sightings (Siebert et al 2006, Pikesley et al 2011). The analysis of land-based data (Chapter IV, Pierce et al 2010) did not find clear seasonal trends in the number of sightings, while results from boat-based surveys (Chapter III) showed higher number of detections in June and October. Thus the seasonal pattern of strandings is probably not directly linked to local distribution.

The distribution of harbour porpoise strandings along the coast of WIP showed an increase in the number of strandings from North to South with two regions showing highest numbers of strandings: SA.5 and SA.9. Both areas were previously identified as having a high number of porpoise strandings (Sequeira 1996, Lens 1997). While SA.5 is the one with fewest sightings (Pierce et al 2010, Chapter IV), SA.9 is also one with most sightings (Santos et al 2012). Usually,

it is expected that areas with highest occurrence of sightings will also be the ones with highest number of strandings, since both might be expected to reflect local abundance. Therefore and especially in Galicia, there may be other factors influencing the arrival of carcasses on the coast, such as oceanographic features (currents, tides, winds, sea-pressure gradients, bottom topography) (Evans et al 2005, Leeney et al 2008, de Boer et al 2012, Peltier et al 2012, 2013), destruction of the carcasses by scavengers (Peltier et al 2012) or the sinking of the body. All these factors mean that not all the dead animals arrive on the shore and/or that, if they do so it is in different areas from where they were living. In the study area there could be a mixture of carcasses originating from i) Asturias and Galicia, ii) different areas of Galicia, iii) Galicia and Portugal, iv) different areas of Portugal, and perhaps less plausibly, v) Gulf of Cádiz, Gibraltar Strait or even North Africa.

In the WIP the key physical environmental factors would be i) the orientation of the coastlines; the ones oriented to the North are less influenced by winds from South and Southwest that are predominant in winter (Cabanas 1999) compared coastlines oriented to the West, so fewer animals will strand in areas oriented to the North in that period of the year; ii) the tidal currents will also influence strandings especially in the mouth of the rías; and in some narrow areas between isles and the tidal range is around 3 m which generates important flow and ebb tide currents (Cabanas 1999) which can drive the carcasses to different areas; iii) on coastlines with more sandy beaches, carcasses may remain for longer periods of time than in steep rocky areas, so they are more likely to be found; iv) the presence of the Portuguese Current, the Navidad Current (Pingree and Le Cann 1989) and the upwelling system, could cause carcasses to travel to different areas from where they were living; v) the presence of storms that are more frequent during autumn and winter, which can carry carcasses also to other areas and also cause the death of animals in poor condition (López et al 2002).

To try to find out the proportion of dead animals that reach the shore in Galicia, a study tagging by-caught animals and releasing them again into the sea was carried out (Martinez-Cedeira et al 2011), and found that nearly 22% reach the shore travelling between 31 and 100 km. In other studies in Europe the proportion of carcasses that reached the shore was lower, however Peltier et al (2012) concluded that although the number of animals that strand is a small fraction of the ones that die over the continental shelf, strandings can allow us to assess mortality both numerically and spatially, as well as relative abundance, species richness and distribution of cetaceans.

The probability of stranding is not the only important issue, the probability of finding the carcasses is important as well. Since 1999 in Galicia and 2000 in Portugal, the effort of Strandings Networks has stabilized, but in later years there may have been an ongoing increase of stranding reports by people present on the beaches due to the ease of access to the authorities, thanks, for example, with the opportunity of using 112 to report strandings and sightings.

Peltier et al (2012) estimated that, under the assumption that all dead carcasses float and drift, the probability that a stranded cetacean is discovered is only around 12.9%. Therefore, a rather small proportion of dead animals are likely to be recorded and necropsied, but they can still provide relevant information on mortality at sea, relative abundance, species richness and distribution of cetaceans (Maldini et al 2005, MacLeod et al 2005, Pyeson 2010, 2011, Peltier et al 2012).

Characteristics of harbour porpoises stranded in the WIP: sex, length and by-catch

Together with the information on presence/absence and spatiotemporal trends, strandings provide data about life history, diet, health, contaminants, genetics or cause of death (e.g. Siebert et al 1999, Jauniaux et al 2002, Santos and Pierce 2003, Das et al 2004 a, b, Santos et al 2004, 2005, Fontaine et al 2007 b, 2014, Murphy et al 2010, Lopez et al 2012, Read et al 2012, Stockin et al 2013, Méndez-Fernández et al 2014 a, b). In the WIP coast the oceanographic features and the situation of the WIP itself reduce the probability of carcasses belonging to other areas reaching this coast; and the isolation of Iberian population from porpoises of other European waters together with the absence of any population structure along the Spanish and Portuguese coasts (Fontaine et al 2007 a, 2010, 2014, Alfonsi et al 2012, Chapter II), suggest that the carcasses will be representative of the animals present in the area.

In the WIP there was the same proportion of males as females, although the number of females was slightly lower in Portugal. The total body length ranged from 81 to 202 cm with a mean length of 146.66 cm, the Portuguese porpoises being larger than Galician, and females larger than males. These sizes agree with previous studies that described the Iberian porpoises as larger animals than those of other areas (e.g. Donovan and Bjørge 1995, Sequeira 1996, Lens 1997, Lockyer 2003, Lopez 2003, Read et al 2012, Lopez et al 2012). The larger animals stranded in winter and carcasses were fresher when animals were smaller. This could be due to the presence of larger animals in areas far from the coast that winter conditions move

closer to the coast, and of smaller animals in areas near the shore which will strand faster and with better body condition than others from farther areas.

By-catch is one of the principal threats for small cetaceans, especially harbour porpoises (IWC 1994). In an area of high fishing effort such as WIP (Sequeria et al 1992, EUROSTAT 2010) interactions between fisheries and cetaceans has become a topic of great concern (e.g. Lopez et al 2002, Fernández-Contreras et al 2010, Ferreira et al 2012, López et al 2012, Read et al 2012, Goetz et al 2014). Relatively few cetacean by-catches are directly reported by fishermen, so this problem has to be studied with observers on board fishing boats, interviews or by diagnosis during the necropsies (absence of tail/flippers, presence of ropes, net marks).

In Galicia, many by-catches are common dolphins (23%), but other species such as harbour porpoises (22%) and bottlenose dolphins (14%) are also by-caught (López et al 2002, 2003). In the current study, it was found that on average 33.42% of the stranded porpoises had signs of by-catch with a higher proportion in the Portuguese coast (55.95%) than in the Galician coast (26.24%). That difference was also highlighted by Read et al (2012) who suggested that one of the reasons could be that gillnets are one of the gears that cause the highest rates of by-catch in Galicia whereas in Portugal, although gillnets are also problematic, the beach-seines are commonly used in North-Central Portugal and are thought to be one of the gears to which harbour porpoises are most vulnerable (Sequeira and Inácio 1992, López and Valeiras 1997, López et al 2003, Ferreira 2007). Ferreira et al (2012) suggested that in Portugal the interaction with fisheries is the cause of 44 - 54% of the registered cetacean deaths, including 58% for porpoises (Ferreira 2007).

Since the detection of signs of by-catch in carcasses depends on the state of decomposition and the amount of animals that reach the shore, the number of cetaceans that die due to interactions with fisheries is probably underestimated if carcasses in poor condition are used to calculate the by-catch rate. Despite that, the rates found indicate that the bycatch mortality is unsustainable, as suggested by Ferreira (2007), López et al (2012), Read et al (2012) and Goetz et al (2014), referring to ASCOBANS (1997), which states that an anthropogenic removal of more than 1.7% of the best available population estimate abundance represents an '*unacceptable interaction*'.

This differentiated and isolated harbour porpoise population of the WIP faces an important problem, and as an area with a great socio-economic importance of fisheries, it is difficult to reduce and likely impossible to totally avoid by-catch. However, measures to reduce that

problem and specific management plans for porpoises should be developed. Different measures can be developed in this area, such as i) the reduction of the use of gears that cause damage to porpoises or restriction of their use in areas where the species has high densities, ii) the use of acoustic deterrent devices ("pingers"), coupled with monitoring of their effectiveness, and iii) of acoustic reflective nets, to reduce the likelihood of entanglement by modifying the behaviour of the animals and increment their ability to detect nets, which have been proved to be effective for porpoises in several areas (see Dawson et al 2013 for a review of the use of pingers, Trippel et al 2003, Larsen et al 2007), and can also reduce the economic cost of damage to nets and captured fish. However, it has to be kept in mind that such devices increase the noise in the sea and there is the possibility of causing the exclusion of the species from areas where they normally feed. Also there could be a reduction of the catch of the target species and reduced ease of handling for fishermen of some modified nets (Trippel et al 2003, Larsen et al 2007, Dawson et al 2013).

Study limitations

When a study is based on non-invasive samples there is a problem related with the number and area coverage of the samples. For harbour porpoise the use of biopsies is complicated due to the shy behaviour of the species, aside from ethical, logistic and financial considerations, therefore usually samples from porpoises come from strandings or fisheries by-catches. This sampling is usually more accessible and provides a low-cost alternative to samples obtained by other techniques (e.g. biopsy sampling) but, as it is known, stranded animals can drift and carcasses can be recovered many kilometres away from their location of death and also they can be in poor body condition. In the present study, samples from stranded animals were used to perform genetic analyses and in all cases stranding location was used as proxy of sample origin. Despite those limitations due to the use of strandings, it was possible to have strong conclusions regarding harbour porpoise genetics. Other limitations relate to the fact that within stranded individuals there might be a relative high proportion of sick or weak individuals that may be more susceptible of stranding, although in the analyses of length and by-catch this should not have any influence, it could have an influence when studying the body condition.

In boat-based surveys GPS positions of the different vessels at the time of each sighting were used as proxy of cetacean location, and in land-based surveys, their position is related to the observation station, which limits the accuracy of assignment of environmental variables to each particular sighting. However, it is likely that most of the sightings of harbour porpoises

were recorded within a small distance from the vessel (i.e. 1 km) minimizing the potential error.

Conclusion

The present study provides some useful data on the genetic characteristics and suitable habitat areas of harbour porpoise in West Iberian Peninsula, with a special focus on North West Iberia. Results provide evidence of an absence of genetic structure along WIP and a clear isolation of this population from the populations of the North East Atlantic and Black Sea with an important influence of the ongoing ecological processes. These results support the recommended definition of Iberian Peninsula as a management units for harbour porpoise proposed for MSFD and also the definition of a third subspecies, *Phocoena phocoena meridionalis*. Both sightings and strandings showed that porpoises are present in the area all year around with variations in the number of sightings between years, months and subareas, which leads us to think that they may move between areas. The results of this study provide essential information about this species in Galicia. For example, i) protected areas cannot be seasonal, because the species is present throughout the year, ii) Galicia is one of the key areas in the Iberian peninsula, with five localities with particularly high occurrence of porpoises: Punta Candieira, Vilán and Touriñán Cape, Punta Remedios (Lira) and Faro de Corrubedo, iii) the main areas used by harbour porpoises and bottlenose dolphins are different, moreover, while a part of the bottlenose dolphin population was described as a resident population (Fernández et al 2011) the porpoise population does not seem to behave in the same way, therefore the same SAC is not going to be useful for both species, unless it is big enough to cover those different areas. Strandings showed that, as was known, harbour porpoises from WIP are bigger that those from other areas, and with similar proportion of males and females. It is well known that by-catch is one of the principal threats for small cetaceans, especially harbour porpoises, and it is of concern in an area of high fishing effort such as WIP. A higher proportion of by-caught porpoises was found on the Portuguese coast than on the Galician coasts, maybe due to the difference in the fishery arts used in each area. In any case, in both areas (Galicia and Portugal) bycatch mortality is unsustainable according to ASCOBANS (1997). However by-catch is not the only threat for this species, and is essential to carry out further studies to enrich the knowledge about Iberian harbour porpoises and to support its conservation.

Future Work.

To increase our knowledge about harbour porpoises in the Iberian Peninsula, several lines of further studies may be suggested:

- Increase the number of samples from WIP and especially from Gulf of Cadiz for an even more fine-scale genetic analyse and including new techniques to provide a genome-wide pattern of genetic divergence across populations to examine the extent to which ecological divergence drives adaptive genetic differentiation as well as neutral divergence.
- The further study of Iberian porpoise diet from stomach contents and other methodologies such as stable isotopes and fatty acid profiles, will help us to interpret the distribution of porpoises in the area.
- A continuous monitoring program from boat and land-based surveys will increase the information about distribution and abundance of the species, and then it will allow a better understanding of the relationship of the distribution of porpoises with environmental variables. Moreover, it will give the opportunity to evaluate the success of conservation strategies for the species.
- The increase the boat-based survey effort with surveys all year around, along the whole Galician coast, reaching deeper areas, and keeping them in time, will give more comparable data with land-based surveys and knowledge about the presence of porpoises in areas poor known until now.
- The analyses of pooled sightings of porpoises from all WIP would give us a better idea of that relationship between its distribution and environment than the study of the areas separately.
- The development of acoustic studies would increase the hours of monitoring and provide useful supplementary data about the distribution of the species even at night.
- An implementation of observation effort in the areas detected as especially used by porpoises will complement the information about the use of those areas by them, giving additional knowledge about this species.
- Study measures to reduce by-catch in the area such as acoustic deterrent devices, acoustic reflective nets, or the reduction of fishing effort in areas of especial use for porpoises.

REFERENCES

ACCOBAMS (2005) *Report of the Joint ACCOBAMS / Pelagos Workshop on Large Whale Ship Strikes in the Mediterranean Sea*. Editors: Mason Weinrich, Simone Panigada, Christophe Guinet. Monaco, 12-15 November 2005. 35pp.

Aguiar Z (2013) Ecologia alimentar do bôto (*Phocoena phocoena*) ao longo da costa continental portuguesa. Mestrado em Recursos Biológicos Aquáticos. Departamento de Biologia. Universidade de Aveiro. Portugal.

Aguilar A, Borrel A and Pastor T (1999) Biological factors affecting variability of persistent pollutant levels in cetaceans. *Journal of Black Sea/Mediterranean Envrionment* (Spceial issue 1): 83–116.

Alfonsi E, Hassani S, Carpentier F-G, Clec'h J Le, Dabin W, Van Canneyt O, Fontaine MC and Jung J-L (2012) A European melting pot of harbour porpoise in the French Atlantic coasts inferred from mitochondrial and nuclear data. *PloS one* 7(9): e44425. doi:10.1371/journal.pone.0044425.

Alonso JM, López A, González AF and Santos MB (2000) Evidence of violent interactions between bottlenose dolphin (*Tursiops truncatus*) and other cetacean species in NW Spain. *European Research on Cetaceans* 14: 105–106.

Alvarez I, de Castro M and Gomez-Gesteira M (2005) Inter- and intra-annual analysis of the salinity and temperature evolution in the Galician Rías Baixas–ocean boundary (northwest Spain). *Journal of Geophysical Research* 110: 14.

Alvarez I, de Castro M, Prego R, Gomez-Gesteira M (2003) Hydrographic characterization of a winter-upwelling event in the Ria of Pontevedra (NW Spain). *Estuarine Coastal and Shelf Science* 56: 869–876.

Alvarez I, Gomez-Gesteira M, Lorenzo MN, Crespo AJC and Dias JM (2010) Comparative analysis of upwelling influence between the western and northern coast of the Iberian Peninsula. *Continental Shelf Research*. Elsevier 1–12.

Álvarez I, Prego R, de Castro M and Varela M (2012) Galicia upwelling revisited: out-of-season events in the rias (1967–2009). *Ciencias Marinas* 38(1B): 143-159.

Amano M and Miyaza (1992) Greographic variation in skulls of the harbour porpoise, *Phocoena phocoena*. *Mammalia* 56: 133-144.

Amaral AR, Beheregaray LB, Bilgmann K, Boutov D, Freitas L, Robertson KM, Sequeira M, Stockin KA, Coelho MM and Möller LM (2012 b) Seascape genetics of a globally distributed, highly mobile marine mammal: the short-beaked common dolphin (genus *delphinus*). *PloS one* 7(2): e31482.

Amaral AR, Beheregaray LB, Bilgmann K, Freitas IS and Mo LM (2012 a) Influences of past climatic changes on historical population structure and demography of a cosmopolitan marine predator, the common dolphin (genus Delphinus). *Molecular ecology* 21(19): 4854–4871.

Ambar I and Fiúza AFG (1994) Some features of the Portugal current system: a poleward slope undercurrent, an upwelling related summer southward flow and an autumn–winter

poleward coastal surface current. In: Katsaros KB, Fiúza AFG, Ambar I (eds) *2nd International Conference on Air-Sea Interaction and on Meterologoy and Oceanography of the Coastal Zone. September 22-27. Boston, USA. American Meterological Society*, p. 286-287.

Âmbar I (2002) Projecto nuclear GLOBEC e a sua importância num contexto nacional. Newsletter IGBP, n.º 2: 1-2.

Amos B, Schlötterer C and Tautz D (1993) Social structure of pilot whales revealed by analytical DNA profiling. *Science* 260: 670–672.

Andersen LW (1993) The population genetics of the harbour porpoise, *Phocoena phocoena*, in Danish waters and part of the North Atlantic. *Marine Biology* 116: 1–7.

Andersen LW, Holm LE, Siegismund HR, Clausen B, Kinze CC and Loeschcke V (1997) A combined DNA-microsatellite and isozyme analysis of the population structure of the harbour porpoise in Danish waters and west Greenland. *Heredity* 78: 270–6.

Andersen LW, Ruzzante DE, Walton M, Berggren P, Bjørge A and Lockyer C (2001) Conservation genetics of harbour porpoises, *Phocoena phocoena*, in eastern and central North Atlantic. *Conservation Genetics* 2: 309–324.

Ansmann IC, Parra GJ, Lanyon JM and Seddon JM (2012) Fine-scale genetic population structure in a mobile marine mammal: inshore bottlenose dolphins in Moreton. *Molecular Ecology*. 21(18):4472-85.

Arbelo M, De Los Monteros AE, Herráez P, Andrada M, Sierra E, Rodríguez F, Jepson PD and Fernández A (2013) Pathology and causes of death of stranded cetaceans in the canary Islands (1999-2005). *Diseases of Aquatic Organisms* 103(2): 87–99.

Arranz P, Borchers DL, de Soto NA, Johnson MP and Cox MJ (2013) A new method to study inshore whale cue distribution from land-based observations. *Marine Mammal Science* 30(2): 810-818.

ASCOBANS (2000) Proceedings of the third meeting of Parties to ASCOBANS. Bristol, United Kingdom. 26 – 28 July.

ASCOBANS (1997) Resolution No. 2: Incidental take of small cetaceans. *Proceedings of the second meeting of the Parties*. ASCOBANS Secretariat. 17-19 November. Bonn, Germany. 67 pp..

Bailey H and Thompson P (2009) Using marine mammal habitat modelling to identify priority conservation zones within a marine protected area. *Marine Ecology Progress Series* 378: 279–287.

Baker JR and Martin AR (1992). Causes of mortality and parasites and incidental lesions in harbour porpoises (*Phocoena phocoena*) from British waters. *Veterinary Record* 130**:** 554–558.

Balcomb KC and Claridge DE (2001) A mass stranding of cetaceans caused by naval sonar in the Bahamas. *Bahamas Journal of Science* 2: 2–12.

Bandelt H-J, Forster P and Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. *Moecularl Bioogy andl Evolution* 16:37-48.

Bañon R, Villegas-ríos D, Serrano A, Mucientes G and Arronte JC (2010) Marine fishes from Galicia (NW Spain): an updated checklist. *Zootaxa* 2667: 1–27.

Barreiro A, ANABAM, López A and Valeiras X (1994) Achegamento á reproducción da toniña (*Phocoena phocoena*) en Galicia. *Eubalaena* 5: 14-20.

Barreiros JP, Teves M and Rodeia J (2006) First record of the harbour porpoise, *Phocoena phocoena* (Cetacea : Phocoenidae) in the Azores (NE Atlantic). *Journal of Ichtiology and Aquatic Biology* 11(2): 45–46.

Baum JK and Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology* 78(4): 699–714.

Belkhir K, Borsa P, Chikhi L, Raufaste N and Bonhomme F (1996-2004) GENETIX 4.05, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier (France).

Benke H, Bräger S, Dähne M, Gallus A, Hansen S, Honnef C, Jabbusch M, Koblitz J, Krügel K, Liebschner A, Narberhaus I and Verfuß U (2014) Baltic Sea harbour porpoise populations: status and conservation needs derived from recent survey results. *Marine Ecology Progress Series* 495: 275–290.

Bennett PM, Jepson PD, Law RJ, Jones BR, Kuiken T, Baker JR, Rogan E and Kirkwood JK (2001) Exposure to heavy metals and infectious disease mortality in harbour porpoises from England and Wales. *Environmental pollution* 112(1): 33–40.

Benoit-Bird KJ and McManus MA. (2012) Bottom-up regulation of a pelagic community through spatial aggregations. *Biology Letters* 8(5): 813–816.

Berggren P, Wade PR, Carlström J and Read AJ (2002) Potential limits to anthropogenic mortality for harbour porpoises in the Baltic region. *Biological Conservation* 103: 313–322.

Berrow S, Brien JO, Connor IO and McGrath D (2007) Abundance estimate and acoustic monitoring of harbour porpoise *Phocoena phocoena* in the Blasket Islands candidate Special Area of Conservation*. Report to the National Parks and Wildlife Service*, 20 pp.

Berrow S, Hickey R, O'Connor I and McGrath D (2014) Density estimates of harbour porpoises *Phocoena phocoena* at eight coastal sites in Ireland. Biology and Environment: *Proceedings of the Royal Irish Academy* DOI: 10.3318/ BIOE.2014.03

Bérubé M and Palsbøll PJ (1996) Identification of se cvx in Cetaceans by multiplexing with three ZFX and ZFY specific primers. *Molecular Ecology* 5: 283–287.

Bérubé M, Aguilar A, Dendanto D, Larsen F, Notarbartolo di Sciara G, Sears R, Sigurjónsson J, Urban-R J and Palsbøll PJ (1998) Population genetic structure of North Atlantic, Mediterranean Sea and Sea of Cortez fin whales, Balaenoptera physalus (Linnaeus 1758): analysis of mitochondrial and nuclear loci. Molecular ecology 7: 585–99.

Bilgmann K, Möller LM, Harcourt RG, Gales R and Beheregaray LB (2008) Common dolphins subject to fisheries impacts in Southern Australia are genetically differentiated: implications for conservation. *Animal Conservation* 11(6): 518–528.

Bilgmann K, Möller LM, Harcourt RG, Gibbs SE and Beheregaray LB (2007) Genetic differentiation in bottlenose dolphins from South Australia : association with local oceanography and coastal geography. *Marine Ecology Progress Series* 341: 265–276.

Bjørge A and Øien N (1995). Distribution and abundance of harbour porpoise, *Phocoenea phocoena*, in Norwegian waters. *Reports of the International Whaling Commission* (Special Issue 16): 89-98.

Bjørge A, Godoy H and Skern-Mauritzen M (2012) Estimated bycatch of harbour porpoise *Phocoena phocoena* in two coastal gillnet fisheries in Norway. *Reports of the International Whaling Commission* 1–11.

Blanco JL and González JL (ed) (1992) Libro rojo de los vertebrados de España. *Icona*. 714 pp.

Boisseau O, Matthews J, Gillespie D, Lacey C, Moscrop A and Ouamari N El (2007) A visual and acoustic survey for harbour porpoises off North-West Africa: further evidence of a discrete population. *African Journal of Marine Science* 29(3): 403–410.

Booth CG, Embling C, Gordon J, Calderan S V and Hammond PS (2013) Habitat preferences and distribution of the harbour porpoise *Phocoena phocoena* west of Scotland. *Marine Ecology Progress Series* 478: 273–285.

Brito C, Vieira N, Sá E and Carvalho I (2009) Cetaceans' occurrence off the west central Portugal coast: a compilation of data from whaling, observations of opportunity and boat-based surveys. *Journal of Marine Animals and Their Ecology* 2(1): 2–5.

Brodie PF (1995) The Bay of Fundy/Gulf of Maine harbour porpoise (*Phocoena phocoena*): some considerations regarding species interactions, energetics, density dependence and bycatch. *Reports of the International Whaling Commission* (Special Issue 16):181-187.

Brunner P, Douglas M and Bernatchez L (1998) Microsatellite and mitochondrial DNA assessment of population structure and stocking effects in Arctic charr Salvelinus alpinus (Teleostei: Salmonidae) from central. *Molecular ecology* 7: 209–223.

Burek KA, Gulland FMD and O'Hara TM (2008) Effects of climate change on arctic marine mammal health. *Ecological Applications* 18(April): S126–S134.

Byrd BL, Hohn AA, Lovewell GN, Altman KM, Barco SG, Friedlaender A, Harms CA, McLellan WA, Moore KT, Rosel PE and Thayer VG (2014) Strandings as indicators of marine mammal biodiversity and human interactions off the coast of North Carolina. *Fishery Bulletin* 112(1): 1–23.

Cabanas JM (1999) Variabilidad temporal en las condiciones oceanográficas de las aguas de la plataforma continental gallega. Algunas consecuencias biológicas. Universidade de Vigo, 155.

Caillat M, Thomas L and Gillespie D (2013) The effects of acoustic misclassification on cetacean species abundance estimation. *The Journal of the Acoustical Society of America* 134(1): 2469–76.

Camphuysen K (2004) The return of the harbour porpoise (*Phocoena phocoena*) in Dutch coastal waters. *Lutra* 47(1): 135–144.

Camphuysen KCJ (2011) Recent trends and spatial patterns in nearshore sightings of harbour porpoises (*Phocoena phocoena*) in the Netherlands (Southern Bight, North Sea), 1990-2010. *Lutra* 54(1): 39–47.

Cañadas A and Hammond P (2006) Model-based abundance estimates for bottlenose dolphins off southern Spain: implications for conservation and management. *Journal of Cetacean Research and Management* 8: 13–27.

Cañadas A and Hammond P (2008) Abundance and habitat preferences of the short-beaked common dolphin *Delphinus delphis* in the southwestern Mediterranean: implications for conservation. *Endangered Species Research* 4: 309–331.

Cañadas A, Sagarminaga R and García Tiscar S (2003) Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. *Deep Sea Research Part I: Oceanographic Research Papers* 49(2002): 2053–2073.

Cañadas A, Sagarminaga R, Stephanis RDE, Urquiola E and Hammond PS (2005) Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquatic Conservation: Marine and Freshwater Ecosystems* 521: 495–521.

Cannas R, Ferrara G, Milano I, Landi M, Cariani A and Addis P (2012) Spatio-temporal genetic variation of Atlantic bluefin tunas from Sardninian and Mediterranean tuna traps. *Collective Volume of Scientific Papers. ICCAT* 67(1): 351–358.

Carlsson J, McDowell JR, Díaz-Jaimes P, Carlsson JEL, Boles SB, Gold JR and Graves JE (2004) Microsatellite and mitochondrial DNA analyses of Atlantic bluefin tuna (*Thunnus thynnus thynnus*) population structure in the Mediterranean Sea. *Molecular ecology* 13(11): 3345–56.

Carretta J V, Taylor BL and Chivers SJ (2001) Abundance and depth distribution of harbor porpoise (*Phocoena phocoena*) in northern California determined from a 1995 ship survey. *Fishery Bulletin* 99: 29–39.

Carrillo M (2007) Los cetáceos en el Atlántico Central y Oriental: diversidad y amenazas a las que se enfrentan en las Islas de la Macaronesia. *Convention on Migratory Species*. Tenerife, Spain.

Catálogo Nacional de Especies Amenazadas. LEY 42/2007, de 13 de diciembre, del Patrimonio Natural y de la Biodiversidad.14 /12/2007. BOE Nº 299 de especies amenazadas.

Caurant F, Amiard J, Amiard-Triquet C and Sairiau P (1994) Ecological and biological factors controlling the concentrations of trace elements (As, Cd, Cu, Hg, Se, Zn) in delphinids *Globicephala melas* from the North Atlantic Ocean. *Marine Ecology Progress Series* 103: 207–219.

Caurant F, Aubail A, Lahaye V, Van Canneyt O, Rogan E, López A, Addink M, Churlaud C, Robert M and Bustamante P (2006) Lead contamination of small cetaceans in European waters-the use of stable isotopes for identifying the sources of lead exposure. *Marine environmental research* 62(2): 131–48.

Chao A and Shen T-J (2010) Program SPADE (Species Prediction And Diversity Estimation). Program and User's Guide published at http://chao.stat.nthu.edu.tw.

Chappuis P (1991) In: Lavoisier, editor. Les Oligoéléments en médecine et biologie. Tecnique et documentation Lavoisier, Paris.

Christensen J and Richardson K (2008) Stable isotope evidence of long-term changes in the North Sea food web structure. *Marine Ecology Progress Series* 368(1998): 1–8.

Christiansen F, Lusseau D, Stensland E and Berggren P (2010) Effects of tourist boats on the behaviour of Indo-Pacific bottlenose dolphins off the south coast of Zanzibar. *Endangered Species Research* 11: 91–99.

Cohen DM, Inada T, Iwamoto T and Scialabba N (1990) Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. *FAO species catalogue*. Vol. 10. FAO.

Collette BB and Parin NV (1986) Belonidae. p. 604-609. In PJP Whitehead, M-L Bauchot, J-C Hureau, J Nielsen and E Tortonese (eds.) Fishes of the north-eastern Atlantic and the Mediterranean, Volume 2. Unesco, Paris.

Consejería de Medio Ambiente y Ordenación del Territorio (2015) Programa de Gestión Sostenible del Medio Marino Andaluz. Informe Regional 2014. Junta de Andalucía. 126pp.

Covelo P, Martínez-Cediera J, Caldas M, Díaz, JI, Palacios G, Ferreira A, Llavona A, Alonso JM and López A (2009) Cetáceos y pinnípedos en Galicia. 10 años de funcionamiento de la red oficial de varamientos (1999-2008). IX Congreso de la Sociedad Española para la Conservación y Estudio de los Mamíferos. 4-7 diciembre. Bilbao, Spain

Covelo P, Martínez-Cedeira JA, Llavona Á, Díaz JI and López A (2015) Strandings of Beaked Whales (Ziphiidae) in Galicia (NW Spain) between 1990 and 2013. *Journal of the Marine Biological Association of the United Kingdom* 1–7. doi:10.1017/S002531541500048X.

Cox TM, Ragen T, Read AJ, Vos E, Baird R, Balcomb K, Barlow J, Caldwell J, Cranford T, Crum L, D'Amico A, D'Spain G, Fernández A, FInneran J, Gentry R, Gerth W, Gulland F, Hildebrand J, Houser D, Hullar T, Jepson P, Ketten D, MacLeod C, Miller P, Moore S, Mountain D, Palka D, Ponganis P, Rommel S, Rowles T, Taylor B, Tyack P, Wartzok D, Gisiner R, Mead J and Benner L (2006) Understanding the impacts of anthropogenic sound on beaked whales. *Journal of Cetacean Research and Management* 7(3): 177–187.

Cox TM, Read AJ, Solow A and Tregenza N (2001) Will harbour porpoises (*Phocoena phocoena*) habituate to pingers? *Journal of Cetacean Research and Management* 3(1): 81–86.

Cox TM and Read AJ (2004) Echolocation behavior of harbor porpoises *Phocoena phocoena* around chemically enhanced gill nets. *Marine Ecology Progress Series* 279: 275–282.

Croll D, Kudela R and Tershy BR (2006) Ecosystem Impact of the decline of large whales in the North Pacific. *Whales, whaling, and ocean ecosystems*, 202 pp.

Cubasch U, Wuebbles D, Chen D, Facchini MC, Frame D, Mahowald N and Winther J-G (2013) Introduction. In: Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker TF, D Qin, G-K Plattner, M Tignor, SK Allen, J Boschung, A Nauels, Y Xia, V Bex and PM Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Culik BM (2004) Review of Small Cetaceans. Distribution, Behaviour, Migration and Threats. Compiled for CMS by. Illustrations by Maurizio Wurtz, Artescienza. UNEP / CMS Secretariat, Bonn, Germany. 343 pp.

Cury P and Shannon L (2004) Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. *Progress in Oceanography* 60(2-4): 223–243.

Das K, Holsbeek L, Browning J, Siebert U, Birkun A and Bouquegneau J-M (2004 a) Trace metal and stable isotope measurements ($\delta^{13}C$ and $\delta^{15}N$) in the harbour porpoise *Phocoena phocoena relicta* from the Black Sea. *Environmental pollution (Barking, Essex : 1987)* 131(2): 197–204.

Das K, Lepoint G, Leroy Y and Bouquegneau JM (2003) Marine mammals from the southern North Sea: feeding ecology data from $\delta^{13}C$ and $\delta^{15}N$ measurements. *Marine Ecology Progress Series* 263: 287–298.

Das K, Siebert U, Fontaine M, Jauniaux T, Holsbeek L and Bouquegneau J (2004 b) Ecological and pathological factors related to trace metal concentrations in harbour porpoises *Phocoena phocoena* from the North Sea and adjacent areas. *Marine Ecology Progress Series* 281: 283–295.

Dawson S, Northridge S, Waples D and Read A (2013) To ping or not to ping: the use of active acoustic devices in mitigating interactions between small cetaceans and gillnet fisheries. *Endangered Species Research* 19(3): 201–221.

de Boer J, Wester PG, Klamer HJC, LewisWE and Boon JP (1998) Do flame retardants threaten ocean life? *Nature* 394: 28–9.

de Boer MN, Saulino JT, Leopold MF, Reijnders PJH and Simmonds MP (2012) Interactions between short-beaked common dolphin (*Delphinus delphis*) and the winter pelagic pair-trawl fishery off Southwest England (UK). *International Journal of Biodiversity and Conservation* 4(13): 481–499.

De Boer MN, Simmonds MP, Reijnders PJH and Aarts G (2014) The influence of topographic and dynamic cyclic variables on the distribution of small cetaceans in a shallow coastal system. *PloS one* 9(1): e86331.

De Luna CJ, Goodman SJ, Thatcher O, Jepson PD, Andersen L, Tolley K and Hoelzel AR (2012) Phenotypic and genetic divergence among harbour porpoise populations associated with habitat regions in the North Sea and adjacent seas. *Journal of evolutionary biology* 25: 674–681.

De Pierrepont JF, Dubois B, Desormonts S, Santos MBO and Robin JPP (2005) Stomach contents of English Channel cetaceans stranded on the coast of Normandy. *Journal of the Marine Biological Association of the United Kingdom* 85: 1539–1546.

Dede A, Ozturk AA and Tonay AM (2008) Cetacean surveys in the Istanbul (Bosphorus) Strait in 2006. In: Proceedings CD of 22nd Annual Conference of European Cetacean Society, Egmond aan Zee, the Netherlands. (eds., GJ Pierce, E Philips, R Lick).

Defaveri J, Viitaniemi H, Leder E and Merilä J (2013) Characterizing genic and nongenic molecular markers: comparison of microsatellites and SNPs. *Molecular ecology resources* 13(3): 377–92.

Delibes M, Rodríguez A and Ferreras P (2000) Action plan for the conservation of the Iberian lynx (*Lynx pardinus*) in Europe. Council of Europe Publishing. *Nature and environment*, No. 111. 44 pp.

Dolman SJ, Hodgins NK, MacLeod CD, Pierce GJ and Weir CR (2013) Harbour porpoises (*Phocoena phocoena*) and minke whales (*Balaenoptera acutorostrata*) observed during land-based surveys in The Minch, north-west Scotland. *Journal of the Marine Biological Association of the United Kingdom* 1994: 1–10.

Donovan G and Bjørge A (1995) Harbour porpoises in the North Atlantic: edited extract from the Report of the IWC Scientific Committe, Dublin 1995. *International Whaling Commission* (Special Issue 16). 25 pp.

Doval MD, Nogueira E, and Pérez FF (1998) Spatio-temporal variability of the thermohaline and biogeochemical properties and dissolved organic carbon in a coastal embayment affected by upwelling: the Ría de Vigo (NW Spain). *Journal of Marine Systems* 14: 135–150.

Dower JF and Perry RI (2001) High abundance of larval rockfish over Cobb seamount, an isolated seamount in the northeast Pacific. *Fisheries Oceanography* 10: 286-274

Dunshea G, Barros NB, Berens McCabe EJ, Gales NJ, Hindell M a, Jarman SN and Wells RS (2013) Stranded dolphin stomach contents represent the free-ranging population's diet. *Biology letters* 9(3): 20121036.

Earl D (2011) Structure Harvester v0.6.1. http://taylor0.biology.ucla.edu/structureHarvester/.

Embling CB, Gillibrand PA, Gordon J, Shrimpton J, Stevick PT and Hammond PS (2010) Using habitat models to identify suitable sites for marine protected areas for harbour porpoises (*Phocoena phocoena*). *Biological Conservation*. Elsevier Ltd 143(2): 267–279.

Engel MH, Marcondes MCC, Martins CCA, Luna FO, Lima RP and Campos A (2004) Are seismic surveys responsible for cetacean strandings ? An unusual mortality of adult Humpback Whales in Abrolhos Bank, Northeastern coast of Brazil. *International Whaling Commission* (SC/56/E28).

Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, Ramey RR and McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecology Letters* 8(10): 1029–1038.

Estes JA, Danner EM, Doak DF, Konar B, Springer a M, Steinberg PD, Tinker MT and Williams TM (2004) Complex trophic interactions in kelp forest ecosystems. *Bulletin of Marine Science* 74(3): 621–638.

Estes JA, Tinker M, Williams T and Doal D (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282(5388): 473–476.

Estes JA (2005) Carnivory and trophic connectivity in kelp forests. In: Ray JC, Redford KH, Steneck RS, Berger J (eds) Large carnivores and the conservation of biodiversity. Washington, DC: Island Press. 61–81 pp.

European Commission (2014) Report from the Commission to the Council and the European Parliament. The first phase of implementation of the Marine Strategy Framework Directive (2008/56/EC). The European Commission's assessment and guidance {SWD (2014) 49 final}).

EUROSTAT (2010) Fishery statistics. Data 1995 – 2008. Eurostat Pocketbooks. European Commission. Publications Office of the European Union, Luxembourg. 56 pp.

Evanno G, Regnaut S and Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular ecology* 14(8): 2611–20.

Evans K, Thresher R, Warneke RM, Bradshaw CJA, Pook M, Thiele D and Hindell MA (2005) Periodic variability in cetacean strandings: links to large-scale climate events. *Biology letters* 1(2): 147–50.

Evans PGH and Hammond PS (2004) Monitoring cetaceans in European waters. *Mammal Review* 34(1-2): 131–156.

Evans PGH and Teilmann J (editors) (2009) Report of ASCOBANS/ HELCOM Small Cetacean Population Structure Workshop. ASCOBANS/ UNEP Secretariat, Bonn, Germany. 140 pp.

Excoffier L and Lischer HEL (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources* 10(3): 564-567.

FAPAS (2013) Perfil genético del núcleo reproductor osero de la zona central de Asturias. Report of the Fondo para la protección de los animales salvajes (FAPAS). Spain. 43 pp.

Fernández A, Arbelo M, Deaville R, Patterson I, Castro P, Baker J, Degollada E, Ross H, Herráez P, Pocknell A, Rodríguez E, Howie F, Espinosa A, Reid R, Jaber J, Martin V, Cunningham A and Jepson P (2004) Pathology: whales, sonar and decompression sickness. *Nature* 428: 1–2.

Fernández A, Edwards JF, Rodríguez F, Espinosa de los Monteros A, Herráez P, Castro P, Jaber JR, Martín V and Arbelo M (2005) 'Gas and fat embolic syndrome' involving a mass stranding of beaked whales (family Ziphiidae) exposed to anthropogenic sonar signals. *Veterinary pathology* 42(4): 446–57.

Fernández A, Sierra E, Martín V, Méndez M, Sacchini S, Bernaldo de Quirós Y, Andrada M, Rivero M, Quesada O, Tejedor M and Arbelo M (2012) Last 'atypical' beaked whales mass stranding in the Canary Islands (July, 2004). *Journal of Marine Science: Research & Development* 02(02).

Fernández R (2010) Ecology of the bottlenose dolphin, *Tursiops truncatus* (Montagu 1821), in Galician waters , NW Spain. PhD Thesis. Universidade de Vigo, Spain.

Fernández R, MacLeod CD, Pierce GJ, Covelo P, López A, Torres-Palenzuela J, Valavanis V and Santos MB (2013) Inter-specific and seasonal comparison of the niches occupied by small cetaceans off north-west Iberia. *Continental Shelf Research*. Elsevier 64: 88–98.

Fernández R, Santos MB, Pierce GJ, Llavona Á, López A, Silva MA, Ferreira M, Carrillo M, Cermeño P, Lens S and Piertney SB (2011) Fine-scale genetic structure of bottlenose dolphins, *Tursiops truncatus*, in Atlantic coastal waters of the Iberian Peninsula. *Hydrobiologia* 670: 111–125.

Fernández-Contreras M, Cardona L, Lockyer CH and Aguilar A (2010) Incidental bycatch of short-beaked common dolphins (*Delphinus delphis*) by pairtrawlers off northwestern Spain. *ICES Journal of Marine Science* 16: 1–7.

Ferrara G, Cannas R, Stagioni M and Riccioni G (2010) Fishery genetics of Mediterranean blueffin tuna: review of existing data, o-going studies and perpectives. *Collective Volume of Scientific Papers. ICCAT* 65(3): 988–995.

Ferreira M (2007) Ocorrência e captura acidental de cetáceos no Centro/Norte de Portugal. Tese de Mestrado: Ciências do Ambiente – Área de Especialização em Qualidade Ambiental. Universidade do Minho. Portugal. 92 pp.

Ferreira M, Marçalo A, Nicolau L, Araújo H, Santos J, Pinheiro C, Lopes T, Mendes S, Vaqueiro J, Medina P, Cascalho A, Sequeira M, Eira C and Vingada J (2012) Estado actual das redes de arrojamentos e de reabilitação em Portugal Continental. Anexo do Relatório intercalar do projecto LIFE MarPro PT/NAT/00038.

Figueiras F, Labarta U and Fernández Reiriz M (2002) Coastal upwelling primary production and mussel growth in the Rías Baixas of Galicia. *Hydrobiologia* 484: 121–131.

Fiúza AF (1983) Upwelling patterns off Portugal. In Coastal Upwelling. pp. 85–87. Eds.: Suess E and Thiede J. Plenum Publishers, New York.

Fontaine MC, Baird SJE, Piry S, Ray N, Tolley KA, Duke S, Birkun A, Ferreira M, Jauniaux T, Llavona A, Oztürk B, A Oztürk A, Ridoux V, Rogan E, Sequeira M, Siebert U, Vikingsson GA, Bouquegneau J-M and Michaux JR (2007 a) Rise of oceanographic barriers in continuous populations of a cetacean: the genetic structure of harbour porpoises in Old World waters. *BMC biology* 5: 30.

Fontaine MC, Roland K, Calves I, Austerlitz F, Palstra FP, Tolley KA, Ryan S, Ferreira M, Jauniaux T, Llavona A, Oztürk B, Oztürk AA, Ridoux V, Rogan E, Sequeira M, Siebert U, Vikingsson GA, Borrell A, Michaux JR and Aguilar A (2014) Postglacial climate changes and rise of three ecotypes of harbor porpoises, *Phocoena phocoena*, in western Palearctic waters. *Molecular ecology* 23(13): 3306–3321.

Fontaine MC, Snirc A, Frantzis A, Koutrakis E, Oztürk B, Oztürk A a and Austerlitz F (2012) History of expansion and anthropogenic collapse in a top marine predator of the Black Sea estimated from genetic data. *Proceedings of the National Academy of Sciences of the United States of America* 109(38): E2569–76.

Fontaine MC, Tolley KA, Michaux JR, Birkun A, Ferreira M, Llavona Á, Öztürk B, Öztürk AA, Ridoux V, Rogan E, Bouquegneau J and Baird SJE (2010) Genetic and historic evidence for climate-driven population fragmentation in a top cetacean predator: the harbour porpoises in European water. *Proceedings of the Royal Society B* 277: 2829–2837.

Fontaine MC, Tolley KA, Siebert U, Gobert S, Lepoint G, Bouquegneau J and Das K (2007 b) Long-term feeding ecology and habitat use in harbour porpoises *Phocoena phocoena* from Scandinavian waters inferred from trace elements and stable isotopes. *BMC biology* 7(1): 1–12.

Ford JKB, Ellis GM, Olesiuk PF and Balcomb KC (2010) Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator? *Biology letters* 6(1): 139–142.

Fraga F (1981) Upwelling of the Galician coast, Northwest Spain. In: Richards F (ed) Coastal Upwelling. *American Geophysical Union Washington*, DC. pp. 176-182.

Frankham R (2005) Genetics and extinction. *Biology Conservation* 126: 131–140.

Frankham R, Ballou JD and Briscoe DA (2002) Introduction to conservation genetics. Cambridge University Press, Cambridge, United Kingdom. 644 pp.

Frantzis A (1998) Does acoustic testing strand whales? *Nature* 392: 29.

Frantzis A, Gordon J, Hassidis G and Komnenoy A (2001) The enigma of harbour porpoise in the Mediterranean sea. *Marine Mammal Science* 17(October): 937–944.

Fullard KJ, Early G, Heide-Jorgensen MP, Bloch D, Rosing-Asvid A and Amos W (2000) Population structure of long-finned pilot whales in the North Atlantic: a correlation with sea surface temperature? *Molecular Ecology* 9:949–958.

Galatius A and Gol'din PE (2011) Geographic variation of skeletal ontogeny and skull shape in the harbour porpoise (*Phocoena phocoena*). *Comparative and General Pharmacology* 89(May): 869–879.

Gannon DP, Craddock JE and Read AJ (1998) Autumn food habits of harbor porpoises, *Phocoena phocoena*, in the Gulf of Maine. *Fishery Bulletin* 96: 428-437.

Garner A, Rachlow JL and Hicks JF (2005) Patterns of genetic diversity and its loss in mammalian populations. *Conservation Biology* 19(4): 1215–1221.

Gaskin DE (1984) The harbour porpoise *Phocoena phocoena* (L.): regional populaions, status, and information on direct and indirect catches. *International Whaling Commission* 34: 569–586.

Gaspari S, Holcer D, Mackelworth P, Fortuna C, Frantzis A, Genov T, Vighi M, Natali C, Rako N, Banchi E, Chelazzi G and Ciofi C (2013) Population genetic structure of common bottlenose dolphins (*Tursiops truncatus*) in the Adriatic Sea and contiguous regions: implications for international conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*. doi: 10.1002/aqc.2415.

Gazo M, Gonzalvo J and Aguilar A (2008) Pingers as deterrents of bottlenose dolphins interacting with trammel nets. *Fisheries Research* 92(1): 70–75.

Geelhoed SC V, Scheidat M, Bemmelen RSA Van and Aarts G (2013) Abundance of harbour porpoises (*Phocoena phocoena*) on the Dutch Continental Shelf, aerial surveys in July 2010-March 2011. *Lutra* 56(1): 45–57.

Genner MJ, Sims DW, Wearmouth VJ, Southall EJ, Southward AJ, Henderson PA and Hawkins SJ (2004) Regional climatic warming drives long−term community changes of British marine fish Regional climatic warming drives long-term community changes of British marine fish. *Proceedings of the National Academy of Sciences of the United States of America* 271: 655–661.

Gil J (2003) Changes in the pattern of water masses resulting from a poleward slope current in the Cantabrian Sea (Bay of Biscay). *Estuarine, Coastal and Shelf Science* 57(5-6): 1139–1149.

Gilles A, Adler S, Kaschner K, Scheidat M and Siebert U (2011) Modelling harbour porpoise seasonal density as a function of the German Bight environment: implications for management. *Endangered Species Research* 14(2): 157–169.

Gilles A, Scheidat M and Siebert U (2009) Seasonal distribution of harbour porpoises and possible interference of offshore wind farms in the German North Sea. *Marine Ecology Progress Series* 383 (June 2008): 295–307.

Gillespie D, Berggren P, Brown S, Kuklik I, Lacey I, Lacey C, Lewis C, Matthews J, McLanaghan R and Tregenza N (2005) Relative abundance of harbour porpoises (*Phocoena phocoena*) from acoustic and visual surveys of the Baltic Sea and adjacent waters during 2001 and 2002. *Journal of Cetacean Research and Management* 7(1): 51–57.

Goetz S, Read FL, Santos MB, Pita C and Pierce GJ (2014) Cetacean–fishery interactions in Galicia (NW Spain): results and management implications of a face-to-face interview survey of local fishers. *ICES Journal of Marine Science* 71: 604-617.

Goetz S, Santos MB, Vingada J, Costas DC, Villanueva AG and Pierce GJ (2015) Do pingers cause stress in fish? An experimental tank study with European sardine, *Sardina pilchardus* (Walbaum, 1792) (Actinopterygii, Clupeidae), exposed to a 70 kHz dolphin pinger. *Hydrobiologia* 749, 83–96.

Gol'din PE (2004) Growth and body size of the harbour porpoise, *Phocoena phocoena* (Cetacea, Phocoenidae), in the Sea of Azov and the Black Sea. *Vestnik Zoologii* 38(4): 59–73.

Gönener S and Bilgin S (2009) The effect of pingers on harbour porpoise, *Phocoena phocoena,* bycatch and fishing effort in the turbot gillnet fishery in the Turkish Black Sea coast. *Turkish Journal of Fisheries and Aquatic Sciences* 157: 151–157.

Goodwin L (2008) Diurnal and tidal variations in habitat use of the harbour porpoise (*Phocoena phocoena*) in Southwest Britain. *Aquatic Mammals* 34(1): 44–53.

Gordon JCD, Gillespie D, Potter J, Simmonds MP and Thompson D (2004) A review of the effects of seismic survey on marine mammals. *Marine Technology Society Journal* 37(4): 14–32.

Goudet J (1995) FSTAT (version 1.2): a computer program to calculate f-statistics. *Journal of Heredity* 86(6):186–485.

Goudet J (2002) FSTAT—a program to estimate and test gene diversities and fixation indices version 2.9.3.2. http://www2.unil.ch/popgen/softwares/fstat.htm.

Güçlüsoy H (2009) The first confirmed report of the harbour porpoise (*Phocoena phocoena*) in the Turkish Aegean Sea. *Marine Biodiversity Records* 1(October): 2006–2007.

Guerra A (1992) Mollusca: Cephalopoda. In: Fauna Ibérica, Vol. 1. Ramos MA, Alba J, Bellés X, Gosálvez J, Guerra A, Macpherson E, Martin F, Serrano J and Templado J (editors). Museo Nacional de Ciencias Naturales (CSIC), Madrid. 327 pp. In Spanish.

Haande S, Rohrlack T, Semyalo RP, Brettum P, Edvardsen B, Lyche-Solheim A, Sørensen K and Larsson P (2011) Phytoplankton dynamics and cyanobacterial dominance in Murchison Bay of Lake Victoria (Uganda) in relation to environmental conditions. *Limnologica - Ecology and Management of Inland Waters* 41(1): 20–29.

Haelters J and Camphuysen K (2009) The harbour porpoise in the southern North Sea: Abundance, threats, and research & management proposals. *Reported commissioned by IFAW (International Fund for Animal Welfare)*. 56 pp.

Haelters J, Kerckhof F, Jacques TG and Degraer S (2011) The harbour porpoise *Phocoena phocoena* in the Belgian part of the North Sea: trends in abundance and distribution. *Belgian Journal od Zoology* 141(July): 75–84.

Hammond PS, Berggren P, Benke H, Borchers DL, Collet A, Heide-Jørgensen MP, Heimlich S, Hiby AR, Leopold MF and Øien N (2002) Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *Journal of Applied Ecology* 39(2): 361–376.

Hammond PS, Macleod K, Berggren P, Borchers DL, Burt L, Cañadas A, Desportes G, Donovan GP, Gilles A, Gillespie D, Gordon J, Hiby L, Kuklik I, Leaper R, Lehnert K, Leopold M, Lovell P, Øien N, Paxton CGM, Ridoux V, Rogan E, Samarra F, Scheidat M, Sequeira M, Siebert U, Skov H, Swift R, Tasker ML, Teilmann J, Van Canneyt O and Vázquez JA (2013) Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. *Biological Conservation* 164: 107–122.

Hanski I and Gaggiotti OE (2004) Ecology, genetics and evolution of metapopulations. Elsevier Academic Press.

Hansson B and Westerberg L (2002) On the correlation between heterozygosity and fitness in natural populations. *Molecular Ecology* 11: 2467–2474.

Harpending HC (1994) Signature of ancient population growth in a low-resolution mitochondrial DNA mismatch distribution. *Human Biology* 66(4): 591–600.

Hastie GD, Wilson B, Wilson LJ, Parson KM, Thompson PM (2004) Functional mechanisms underlying cetacean distribution patterns: hotspots for bottlenose dolphins are linked to foraging. *Marine Biology* 144: 397-403.

Hastie TJ and Tibshirani RJ (1990) Generalised Additive Models. Chapman and Hall, London. 335 pp.

Heide-Jørgensen MP (2013) Correction of at-surface abundance of harbour porpoises in West Greenland based on detection to 1 m depth. *NAMMCO SC/20/HP/11 Harbour porpoise Working Group.* November 2013.

Heide-Jørgensen MP, Iversen M, Nielsen NH, Lockyer C, Stern H and Ribergaard MH (2011) Harbour porpoises respond to climate change. *Ecology and evolution* 1(4): 579–85.

Heide-Jørgensen MP, Richard P, Ramsay M and Akeeagok S (2002) Three recent ice entrapments of Arctic cetaceans in West Greenland and the eastern Canadian High Arctic. *NAMMCO Sci. Publ.* 4:143-148.

Hewitt G (2000) The genetic legacy of the Quaternary ice ages. *Nature* 405(6789): 907–13.

Hoek W (1992) An unusual aggregation of harbour porpoises (*Phocoena phocoena*). *Marine Mammal Science* 8:152-155.

Hoelzel RA, Natoli A, Dahlheim ME, Olavarria C, Baird RW and Black NA (2002) Low worldwide genetic diversity in the killer whale (*Orcinus orca*): implications for demographic history. *Proceedings. Biological sciences / The Royal Society* 269(1499): 1467–73.

Hoelzel RA, Potter CW and Best PB (1998) Genetic differentiation between parapatric "nearshore" and "offshore" populations of the bottlenose dolphin. *Proceedings of the Royal Society B* 265(1402): 1177–83.

Höglund J (2009) Evolutionary conservation genetics. Oxford University Press Inc., New York.

Hooker SK, Whitehead H and Gowans S (1999) Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. *Conservation Biology* 13(3): 592–602.

Huthnance JM, Van Aken HM, White M, Barton ED, Le Cann B, Ferreira Coelho E, Alvarez Fanjul E, Miller P and Vitorino J (2002) Ocean margin exchange — water f lux estimates. *Journal of Marine Systems* 32: 107–137.

ICES (2012) Report of the ICES Advisory Committee 2012. ICES Advice, 2012. Book 7. 205 pp.

ICES (2013) Report of the Working Group on Marine Mammal Ecology (WGMME), 4– 7 February 2013, Paris, France. ICES CM 2013/ACOM:26. 117 pp

ICES (2014) Report of the Working Group on Marine Mammal Ecology (WGMME), 10–13 March 2014, Woods Hole, Massachusetts, USA. ICES CM 2014/ACOM: 27. 228 pp.

Isojunno S, Matthiopoulos J and Evans P (2012) Harbour porpoise habitat preferences: robust spatio-temporal inferences from opportunistic data. *Marine Ecology Progress Series* 448: 155–170.

IWC (1994) Report of the workshop on mortality of cetaceans in passive fishing nets and traps. *Report of the International Whaling Commission* (Spec Issue 15): 6−71.

IWC (1998) Report of the Scientific Committee. Report of the International Whaling Commission 48: 53-302.

IWC (2012) Report of the Conservation Committee. *International Whaling Commission* IWC/64/Rep (June): 1–18.

Jakobsson M and Rosenberg NA (2007) CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics* 23(14):1801–1806.

Jansen OE, Aarts GM, Das K, Lepoint G, Michel C and Reijnders PJH (2012) Feeding ecology of harbour porpoises: stable isotope analysis of carbon and nitrogen in muscle and bone. *Marine Biology Research* 8: 829–841.

Jauniaux T, Petitjean D, Brenez C, Borrens M, Brosens L, Haelters J, Tavernier T and Coignoul F (2002) Post-mortem findings and causes of death of harbour porpoises (*Phocoena phocoena*) stranded from 1990 to 2000 along the coastlines of Belgium and Northern France. *Journal of comparative pathology* 126(4): 243–53.

Jefferson TA and Curry BE (1994) A global review of porpoise (Cetacea: Phocoenidae) mortality in gillnets. *Biological Conservation* 67: 167–183.

Jepson P (ed), Sabin R, Spurrier C, Jepson P, Deaville R, Perkins M, Cunningham A, Reid R, Patterson I, Barley J, Penrose R and Law R (2005) Trends in cetacean strandings around the UK coastline and cetacean and marine turtle investigations 2000 to 2004 inclusive (Contract CRO 238), Cetaceans Strandings Investigation and Co-ordination in the UK. Department for Environment, Food and Rural Affairs. UK. 142 pp.

Jepson PD and Baker JR (1998) Bottlenosed dolphins (*Tursiops truncatus*) as a possible cause of acute traumatic injuries in porpoises (*Phocoena phocoena*). *The Veterinary record* 28: 614–616.

Jepson PD, Arbelo M, Deaville R, Patterson IAP, Castro P, Baker JR, Degollada E, Ross HM, Herraez P, Pocknell AM, Rodriguez F, Howie FE, Espinosa A, Reid RJ, Jaber JR, Martin V, Cunningham AA and Fernandez A (2003) Gas-bubble lesions in stranded cetaceans – was sonar responsible for a spate of whale deaths after an Atlantic military exercise? *Nature* 425: 575–576.

Jepson PD, Baker JR, Kuiken T, Simpson V, S K and Bennett PM (2000) Pulmonary pathology of harbour porpoises (*Phocoena phocoena*) stranded in England and Wales between 1990 and 1996. *Veterinary Record2* 146: 721–728.

Jepson PD, Deaville R, Patterson IAP, Pocknell AM, Ross HM, Baker JR, Howie FE, Reid RJ, Colloff A and Cunningham AA (2005) Acute and chronic gas bubble lesions in cetaceans stranded in the United Kingdom. *Veterinary pathology* 305(42): 291–305.

Jin X, Li YM, Wang Q, Liu ZH, Wang YF, Zhang H, Jin B, Xu YF and Xu X (2011) Primary productivity evaluation based on underwater light distribution in Chaohu Lake. *Huan Jing Ke Xue* 32(5): 1257–1265.

Johnson JA, Toepfer JE and Dunn PO (2003) Contrasting patterns of mitochondrial and microsatellite population structure in fragmented populations of greater prairie-chickens. *Molecular Ecology* 12(12): 3335–3347.

Johnson WE, Godoy J, Palomares F, Delibes M, Fernandez M, Revilla E and O'Brien S (2004) Phylogenetic and phylogeographic analysis of Iberian lynx populations. *Journal of Heredity* 95(1): 19–28.

Johnston D, Westgate A and Read A (2005) Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy. *Marine Ecology Progress Series* 295: 279–293.

Jørgensen HBH, Hansen MM, Bekkevold D, Ruzzante DE, Loeschcke V (2005) Marine landscapes and population genetic structure of herring (*Clupea harengus* L.) in the Baltic Sea. *Molecular Ecology* 14:3219-3234.

Jost L (2008) GST and its relatives do not measure differentiation. *Molecular Ecology* 17:4015–4026.

Jung J-L, Stéphan E, Louis M, Alfonsi E, Liret C, Carpentier F-G and Hassani S (2009) Harbour porpoises (*Phocoena phocoena*) in north-western France: aerial survey, opportunistic sightings and strandings monitoring. *Journal of the Marine Biological Association of the United Kingdom* 89(05): 1045-1050.

Kannan K, Blakenship AL, Jones PD and Giesy JP (2000) Toxicity reference values for the toxic effects of polychlorinated biphenyls to aquatic mammals. *Human and Ecological Risk Assessment* 6: 181–201.

Kastelein RA, Hardeman J and Boer H (1997) Food consumption and body weight of harbour porpoises (*Phocoena phocoena*). In: Read A, Wipkema P and Nachtigall P (eds) *The biology of the harbour porpoise*. Woerden, The Netherlands: De Spil, 217–234.

Keiper C, Ainley D, Allen S and Harvey J (2005) Marine mammal occurrence and ocean climate off central California, 1986 to 1994 and 1997 to 1999. *Marine Ecology Progress Series* 289: 285–306.

Khanna D, Bhutiani R and Chandra K (2009) Effect of the euphotic depth and mixing depth on phytoplanktonic growth mechanism. *International Journal of Environmental Research* 3(2): 223–228.

Kinzie CC (1985) Intraspecific variation in Baltic and North Sea harbour porpoises (*Phocoena phocoena* (L., 1758)). Videnskabelige Meddelelsser fra Dansk Naturhistorie Forening 146:63-74.

Kirk JTO (2011) Light and photosynthesis in aquatic ecosystems (3rd ed.). New York, USA: Cambridge University Press.

Kirkpattrick BW (1992) Identification of a conserved microsatellite site in porcine and bovine insulin-like growth factor-I gene 5p flank. *Animal Genetics* 23: 543–548.

Kirkwood JK, Bennett PM, Jepson PD, Kuiken T, Simpson VR and Baker JR (1997) Entanglement in fishing gear and other causes of death in cetaceans stranded on the coasts of England and Wales. *Veterinary Record* 141**:** 94–98.

Kiszka J, Macleod K, Canneyt O Van, Walker D and Ridoux V (2007) Distribution, encounter rates, and habitat characteristics of toothed cetaceans in the Bay of Biscay and adjacent waters from platform-of-opportunity data. *ICES Journal of Marine Science* 64(5): 1033–1043.

Kocher T, Thomas W, Meyer A, Edwards S, Pââbo S, Villablanca F and Wilson AC (1989) Dynamics of mitochondrial DNA evolution in animals : amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences of the United States of America* 86(August): 6196–6200.

Kocijan I, Galov A, Ćetković H, Kusak J, Gomerčić T and Huber Đ (2011) Genetic diversity of Dinaric brown bears (*Ursus arctos*) in Croatia with implications for bear conservation in Europe. *Mammalian Biology - Zeitschrift für Säugetierkunde* 76(5): 615–621.

Koopman HNK (1998) Topographical distribution of the blubber of harbor porpoises (*Phocoena phocoena*). *Journal of Mammaogy*. 79(1):260-270.

Kraaijeveld-Smit FJL, Beebee TJC, Griffiths RA, Moore RD and Schley L (2005) Low gene flow but high genetic diversity in the threatened Mallorcan midwife toad *Alytes muletensis*. *Molecular ecology* 14(11): 3307–15.

Kuiken T and Garcia Hartmann M (1991) Proceedings of the first European Cetacean Society workshop on 'Cetacean pathology: dissection techniques and tissue sampling'. *ECS Newslett* 17: 1–39.

Kuiken T, Simpson VR, Allchin CR, Bennett PM, Codd GA, Harris EA, Howes GJ, Kennedy S, Kirkwood JK, Law RJ and et al (1994) Mass mortality of common dolphins (*Delphinus delphis*) in south west England due to incidental capture in fishing gear. *Veterinary Record* 134:81-89 doi:10.1136/vr.134.4.81

Kyhn LA, Jørgensen PB, Carstensen J, Bech NI, Tougaard J, Dabelsteen T and Teilmann J (2015) Pingers cause temporary habitat displacement in the harbour porpoise *Phocoena phocoena*. *Marine Ecology Progress Series* 526: 253–265.

Lacy RC (1997) Importance of genetic variation to the viability of mammalian population. *Journal of Mammalogy* 78(2): 320–335.

Laidre KL, Stirling I, Lowry LF, Wiig O, Heide-Jørgensen MP and Ferguson SH (2008) Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological applications : a publication of the Ecological Society of America* 18(2 Suppl): S97–125.

Lambeck RJ (1997) Focal species: A multi-species umbrella for nature conservation. *Conservation Biology* 11(4): 849–56.

Lambert E, MacLeod C, Hall K, Brereton T, Dunn T, Wall D, Jepson P, Deaville R and Pierce GJ (2011) Quantifying likely cetacean range shifts in response to global climatic change: implications for conservation strategies in a changing world. *Endangered Species Research* 15(3): 205–222.

Lambert E, Pierce GJ, Hall K, Brereton T, Dunn TE, Wall D, Jepson PD, Deaville R and Macleod CD (2014) Cetacean range and climate in the eastern North Atlantic: Future predictions and implications for conservation. *Global Change Biology* 20: 1782–1793.

Lande R (1988) Genetics and demography in biological conservation. *Science*, New Series 241(4872): 1455–1460.

Lande R (1998) Anthropogenic, Ecological and genetic factors in extinction and conservation anthropogenic factors ecological factors environmental fluctuations and catastrophes. *Researches on Population Ecology* 40(3): 259–269.

Larsen F, Eigaard OR and Tougaard J (2007) Reduction of harbour porpoise (*Phocoena phocoena*) bycatch by iron-oxide gillnets. *Fisheries Research* 85: 270–278.

Lassalle G, Gascuel D, Le Loc'h F, Lobry J, Pierce GJ, Ridoux V, Santos MB, Spitz J and Niquil N (2012) An ecosystem approach for the assessment of fisheries impacts on marine top predators: the Bay of Biscay case study. *ICES Journal of Marine Science* 69(6): 925–938.

Law RJ, Barry J, Barber JL, Bersuder P, Deaville R, Reid RJ, Brownlow A, Penrose R, Barnett J, Loveridge J, Smith B and Jepson PD (2012) Contaminants in cetaceans from UK waters: status as assessed within the cetacean strandings investigation programme from 1990 to 2008. *Marine Pollution Bulletin* 64(7): 1485–1494.

Law RJ, Barry J, Bersuder P, Barber JL, Deaville R, Reid RJ and Jepson PD 2010 Levels and trends of brominated diphenyl ethers in blubber of harbor porpoises (*Phocoena phocoena*) from the UK, 1992–2008. *Environmental Science and Technology* 44, 4447–4451.

Law JR (1996) Metals in marine mammals. In: Beyer WN, Heinz GH, Redmond-Norwood AW, editors. Environmental contaminants in wildlife: interpreting tissue concentrations. US: CRC Press.

Learmonth JA, Murphy S, Luque PL, Reid RJ, Patterson IAP, Brownlow A, Ross HM, Barley JP, Begoña Santos M and Pierce GJ (2014) Life history of harbor porpoises (*Phocoena phocoena*) in Scottish (UK) waters. *Marine Mammal Science* 20(4): 1427–1455.

Learmonth JA, Macleod CD, Santos MB, Pierce GJ and Robinson RA (2006) Potential effects of climate change on marine mammals. *Oceanography and Marine Biology: an Annual Review* 44: 431–464.

Leeney RH, Amies R, Broderick AC, Witt MJ, Loveridge J, Doyle J and Godley BJ (2008) Spatio-temporal analysis of cetacean strandings and bycatch in a UK fisheries hotspot. *Biodiversity and Conservation* 17(10): 2323–2338.

Leeney RH, Witt MJ, Broderick AC, Buchanan J, Jarvis DS, Richardson PB and Godley BJ (2011) Marine megavertebrates of Cornwall and the Isles of Scilly: relative abundance and distribution. *Journal of the Marine Biological Association of the United Kingdom* 1–11.

Lens S (1997) A note on the harbour porpoise in the coastal waters of Spain *Report of the International Whaling Commission* 47: 841-847.

Levitus S, Antonov JI, Boyer TP and Stephens C (2000) Warming of the world ocean. *Science* 287:2225–2229.

Librado P and Rozas J (2009) DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 25:1451–1452.

Lockyer C (1995) Investigation os aspects of the life history of the harbour porpoise, *Phocoena phocoena*, in Brithish Waters. *Report to the International Whaling Commision* (Special Issue16): 199-209.

Lockyer C (2003) A review of methods for defining population structure in the harbour porpoise (*Phocoena phocoena*). In: Haug T, Desportes G, Vikingsson G, Witting L (eds). Harbour porpoises in the North Atlantic. 41-70.

Lockyer C (2007) All creatures great and smaller: a study in cetacean life history energetics. *Journal of the Marine Biological Association of the UK* 87(04): 1035.

Lockyer C and Kinze C (2003) Status, ecology and life history of the harbour porpoise (*Phocoena phocoena*) in Danish waters. In: Haug T, Desportes G, Vikingsson G, Witting L (eds). Harbour porpoises in the North Atlantic. *NAMMCO Sci. Publ.* 5:143-175.

Lockyer C, Desportes G, Hansen K, Labberté S and Siebert S (2003) Monitoring growth and energy utilisation of the harbour porpoise (*Phocoena phocoena*) in human care. In: Haug T, Desportes G, Vikingsson G, Witting L (eds). Harbour porpoises in the North Atlantic. *NAMMCO Sci. Publ.* 5: 107-120.

Lockyer C, Heide-Jørgensen MP, Jensen J, Kinze CC and Sorensen TB (2001) Age, length and reproductive parameters of habour porpoise, *Phocoena phocoena* (L.) from West Greenland. *ICES Journal of Marine Science* 58: 154–162.

López A, Vázquez JA, Martinez-Cedeira JA, Marcos-Ipiña E, Laria L, Maestre I, Carbó A, Llavona A, Fernández M, Díaz JI, Santos L, Ruano A, Fernández R and Méndez P (2012) Bases para el desarrollo de los planes de conservación de las especies de cetáceos protegidas en la Demarcación Marina Noratlántica. Ministerio de Agricultura, Alimentación y Medio Ambiente – Fundación Biodiversidad.

López A (2003) Estatus dos pequenos cetáceos da plataforma de Galicia. PhD Thesis. Universidade de Santiago de Compostela. 337 pp.

López A and Rodriguez A (1995) Agresión de arroás (*Tursiops truncatus*) a toniña (*Phocoena phocoena*). *Eubalaena* 6: 23–27.

López A and Valeiras X (1997) Cause of mortality and suspected by-catches by gross postmortem examination of cetacean strandings on the Galician coast (NW Spain). *European Research on Cetaceans* 11: 42-44.

Lopez A, Pierce G, Santos M, Garcia J and Guerra A (2003) Fishery by-catches of marine mammals in Galician waters: results from on-board observations and an interview survey of fishermen. *Biological Conservation* 111(1): 25–40.

Lopez A, Pierce GJ, Valeiras X, Santos M and Guerra A (2004) Distribution patterns of small cetaceans in Galician waters. *Journal of the Marine Biological Association of the UK* 84(1): 283–294.

Lopez A, Santos MB, Pierce GJ, González AF, Valeiras X and Guerra A (2002) Trends in strandings and by-catch of marine mammals in north-west Spain during the 1990s. *Journal of the Marine Biological Association of the UK* 82(3): 513–521.

López A, Vázquez JA, Martínez-Cedeira J, Cañadas A, Marcos E, Maestre I, Ruano A, Laria L, LLavona A, MaCleod K and Evans P (2013) Abundance estimates for harbour porpoise (*Phocoena phocoena*) in the Spanish area of the Iberian Peninsula Management Unit. *Journal of Cetacean Research and Management* SC/65a/SM20.

Lusseau D (2006) The short-term behavioral reactions of bottlenose dolphins to interactions with boats in Doubtful Sound, New Zealand. *Marine Mammal Science* 22(4): 802–818.

MacLeod C (2009) Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis. *Endangered Species Research* 7(May): 125–136.

MacLeod CD, Bannon S, Pierce GJ, Schweder C, Learmonth J, Herman J and Reid R (2005) Climate change and the cetacean community of north-west Scotland. *Biological Conservation* 124(4): 477–483.

MacLeod CD, Brereton T and Martin C (2009) Changes in the occurrence of common dolphins, striped dolphins and harbour porpoises in the English Channel and Bay of Biscay. *Journal of the Marine Biological Association of the United Kingdom* 89(05): 1059.

Macleod CD, Macleod R, Learmonth JA, Cresswell W and Pierce GJ (2014) Predicting population-level risk effects of predation from the responses of individuals. *Ecology* 95(7): 2006–2015.

MacLeod CD, Pierce GJ and Begoña Santos M (2007 a) Starvation and sandeel consumption in harbour porpoises in the Scottish North Sea. *Biology Letters* 3(5): 535–536.

MacLeod CD, Santos MB, Reid RJ, Scott BE and Pierce GJ (2007 b) Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: could climate change mean more starving porpoises? *Biology letters* 3(2): 185–8.

Madsen PT, Wahlberg M, Tougaard J, Lucke K and Tyack P (2006) Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs. *Marine Ecology Progress Series* 309: 279–295.

Mahfouz C, Henry F, Courcot L, Pezeril S, Bouveroux T, Dabin W, Jauniaux T, Khalaf G and Amara R (2014 a) Harbour porpoises (*Phocoena phocoena*) stranded along the southern North Sea: an assessment through metallic contamination. *Environmental research* 133: 266–273.

Mahfouz C, Henry F, Jauniaux T, Khalaf G and Amara R (2014 b) Organochlorines in harbour porpoises (*Phocoena phocoena*) stranded along the southern North Sea between 2010 - 2013. *Environmental Sciences: Processes and Impacts*. DOI: 10.1039/C4EM00490F.

Maldini D, Mazzuca L and Atkinson S (2005) Odontocete stranding patterns in the main Hawaiian Islands (1937-2002): How do they compare with live animal surveys? *Pacific Science* 59(1): 55–67.

Marques T A, Munger L, Thomas L, Wiggins S and Hildebrand JA (2011) Estimating North Pacific right whale *Eubalaena japonica* density using passive acoustic cue counting. *Endangered Species Research* 13: 163–172.

Marques TA, Thomas L, Ward J, DiMarzio N and Tyack PL (2009) Estimating cetacean population density using fixed passive acoustic sensors: an example with Blainville's beaked whales. *The Journal of the Acoustical Society of America* 125: 1982–1994.

Martin V, Montero R and Heimlich-Boram J (1992) A preliminary observations on the cetological fauna of the Canary Islands. *Proceedings of the 6th Annual Congference of the European Cetacean Society*. 20-22 February. San Remo, Italy.

Martínez-Cedeira JA, Morales X, García JA, Parada A, Covelo P and López A (2011) How many strand? Offshore marking and coastal recapture of cetacean carcasses. *25th Annual Conference of the European Cetacean Society*. 21-23 March. Cádiz, Spain.

Marubini F, Gimona A, Evans P, Wright P and Pierce G (2009) Habitat preferences and interannual variability in occurrence of the harbour porpoise *Phocoena phocoena* off northwest Scotland. *Marine Ecology Progress Series* 381: 297–310.

Mason E, Coombs S and Oliveira PB (2005) An overview of the literature concerning the oceanography of the eastern North Atlantic region. *Relatórios Científicos e Técnicos IPIMAR, Série digital* 33: 58. (http://ipimar-iniap.ipimar.pt)

Mellinger D, Stafford K, Moore S, Dziak R and Matsumoto H (2007) An overview of fixed passive acoustic observation methods for cetaceans. *Oceanography* 20(4): 36–45.

Mendez M, Rosenbaum HC, Subramaniam A, Yackulic C and Bordino P (2010) Isolation by environmental distance in mobile marine species: molecular ecology of franciscana dolphins at their southern range. *Molecular ecology* 19(11): 2212–28.

Mendez M, Subramaniam A, Collins T, Minton G, Baldwin R, Berggren P, Särnblad A, Amir OA, Peddemors VM, Karczmarski L, Guissamulo A and Rosenbaum HC (2011) Molecular ecology meets remote sensing: environmental drivers to population structure of humpback dolphins in the Western Indian Ocean. *Heredity* 107: 349–361.

Méndez-Fernandez P, Pierce GJ, Bustamante P, Chouvelon T, Ferreira M, González AF, López A, Read FL, Santos MB, Spitz J, Vingada JV and Caurant F (2013) Ecological niche segregation among five toothed whale species off the NW Iberian Peninsula using ecological tracers as multi-approach. *Marine Biology* 160(11): 2825–2840.

Méndez-Fernandez P, Webster L, Chouvelon T, Bustamante P, Ferreira M, González AF, López A, Moffat CF, Pierce GJ, Read FL, Russell M, Santos MB, Spitz J, Vingada JV and Caurant F (2014 b) An assessment of contaminant concentrations in toothed whale species of the NW Iberian Peninsula: Part II. Trace element concentrations. *The Science of the total environment.* 484: 206–2017.

Méndez-Fernandez P, Webster L., Chouvelon T, Bustamante P, Ferreira M, González AF, López A, Moffat CF, Pierce GJ, Read FL, Russell M, Santos MB, Spitz J, Vingada JV and Caurant F (2014 a) An assessment of contaminant concentrations in toothed whale species of the NW Iberian Peninsula: Part I. Persistent organic pollutants. *The Science of the total environment.* 484: 196–205.

Merrick RL (1997) Current and historical roles of apex predators in the Bering Sea ecosystem. *Journal of Northwest Atlantic Fishery Science* 22: 343–355.

Mills LS and Smouse PE (1994) Demographic consequences of inbreeding in remnant populations. *The American Naturalist* 144: 412–431.

Miyazaki N, Amano M and Fujise Y (1987) Growth and skull morphology of the harbour porpoises in the Japanese waters. *Memories of the Natural Science Museum of Tokyo* 20: 167-146.

Möller L, Valdez FP, Allen S, Bilgmann K, Corrigan S and Beheregaray LB (2011) Fine-scale genetic structure in short-beaked common dolphins (*Delphinus delphis*) along the East Australian Current. *Marine Biology* 158(1): 113–126.

Möller LM, Wiszniewski J, Allen SJ and Beheregaray LB (2007) Habitat type promotes rapid and extremely localised genetic differentiation in dolphins. *Marine and Freshwater Research* 58(7): 640.

Mooney TA, Au WWL, Nachtigall PE and Trippel EA (2007) Acoustic and stiffness properties of gillnets as they relate to small cetacean bycatch. *ICES Journal of Marine Science* 64: 1324–1332.

Moore SE (2008) Marine mammals as ecosystem sentinels. *Journal of Mammalogy* 89(3): 534–540.

Morissette L, Christensen V and Pauly D (2012) Marine Mammal Impacts in Exploited Ecosystems: Would Large Scale Culling Benefit Fisheries? *PLoS ONE* 7(9).

Moritz C (1994) Applications of mitochondrial DNA analysis in conservation: a critical review. *Molecular Ecology* 3: 401–411.

Morris-Pocock JA, Taylor SA, Birt TP, Damus M, Piatt JF, Warheit KI and Friesen VL (2008) Population genetic structure in Atlantic and Pacific Ocean common murres (*Uria aalge*): natural replicate tests of post-Pleistocene evolution. *Molecular Ecology* 17(22): 4859–73.

Murphy S (2008) Contract Report Investigating biological parameters in common dolphins and harbour porpoises. Final Report to the Department for Environment Food and Rural Affairs Project MF0736. June. 38 pp.

Murphy S, Barber JL, Learmonth JA, Read FL, Deaville R, Perkins MW, Brownlow A, Davison N, Penrose R, Pierce GJ, Law RJ and Jepson PD (2015) Reproductive failure in UK harbour porpoises *Phocoena phocoena*: legacy of pollutant exposure? *PLoS one* 10(7): e0131085. doi:10.1371/journal.pone.0131085

Murphy S, Pierce GJ, Law RJ, Bersuder P, Jepson PD, Learmonth J a, Addink M, Dabin W, Santos MB, Deaville R, Zegers BN, Mets A, Rogan E, Ridoux V, Reid RJ, Smeenk C, Jauniaux T, López A, Alonso Farré JM, González AF, Guerra A, García-Hartmann M, Lockyer C and Boon JP (2010) Assessing the effect of persistent organic pollutants on reproductive activity in common dolphins and harbour porpoises. *Journal of Northwest Atlantic Fishery Science* 42(May): 153–173.

Murphy S, Winship A, Dabin W, Jepson P, Deaville R, Reid R, Spurrier C, Rogan E, López A, González A, Read F, Addink M, Silva M, Ridoux V, Learmonth J, Pierce G and Northridge S

(2009) Importance of biological parameters in assessing the status of *Delphinus delphis*. *Marine Ecology Progress Series* 388: 273–291.

Muus BJ and Nielsen JG (1999) Sea fish. Scandinavian fishing year book, Hedehusene, Denmark. 340 pp.

NAMMCO (North Atlantic Marine Mammal Commission) (1998) Report of the Scientific Committee Working Group on Abundance Estimates. NAMMCO Annual Report 1997, pp. 173–202.

NAMMCO (North Atlantic Marine Mammal Commission) (2013) Report of the Twentieth Meeting of the Scientific Committee, 13-16 November 2013, Reykjavik, Iceland. 90 pp.

Natoli A, Birkun A, Aguilar A, Lopez A and Hoelzel AR (2005) Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society B* 272(1569): 1217–26.

Navia A, Cortés E and Jordán F (2012) Changes to marine trophic networks caused by fishing. INTECH Open Access Publisher.

Newson S, Mendes S, Crick H, Dulvy N, Houghton J, Hays G, Hutson A, Macleod C, Pierce G and Robinson R (2009) Indicators of the impact of climate change on migratory species. *Endangered Species Research* 7(May): 101–113.

Nickel J and Cursons R (2012) Genetic diversity and population structure of the pot-belly seahorse *Hippocampus abdominalis* in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 46(2): 207–218.

Northridge S, Kingston A, Mackay A and Lonergan M (2011) Bycatch of Vulnerable species: understanding the process and mitigating the impacts. Final report to Defra Marine and Fisheries Science Unit, Project no MF1003. University of St Andrews. Defra, London, 99 pp.

Notarbartolo-di-sciara G, Agardy T, Hyrenbach D, Scovazzi T and Van Klaveren P (2008) The Pelagos Sanctuary for Mediterranean marine mammals. *Tethys* 18: 367–391.

Nowacek DP, Thorne LH, Johnston DW and Tyack PL (2007) Responses of cetaceans to anthropogenic noise. *Mammal Review* 37(2): 81–115.

Ólafsdóttir D, Víkingsson GA, Halldórsson SD and Sigurjónsson J (2002) Growth and reproduction in harbour porpoises (*Phocoena phocoena*) in Icelandic waters. In: Haug T, Desportes G, Vikingsson G, Witting L (eds). Harbour porpoises in the North Atlantic. *NAMMCO Sci. Publ.* 5: 195-210.

Orphanides C and Palka D (2013) Analysis of harbor porpoise gillnet bycatch, compliance, and enforcement trends in the US northwestern Atlantic, January 1999 to May 2010. *Endangered Species Research* 20(3): 251–269.

OSPAR (2010) Quality Status Report 2010. London: OSPAR Commission.

OSPAR (2000) Quality status report 2000: Region IV - Bay of Biscay and Iberian Coast. OSPAR Commission, London , UK.

Österblom H, Hansson S, Larsson U, Hjerne O, Wulff F, Elmgren R and Folke C (2007) Human-induced trophic cascades and ecological regime shifts in the Baltic sea. *Ecosystems* 10(6): 877–889.

Oswald JN, Rankin S, Barlow J and Lammers MO (2007) A tool for real-time acoustic species identification of delphinid whistles. *The Journal of the Acoustical Society of America* 122(July): 587–595.

Otero J, Álvarez-Salgado XA, González AF, Gilcoto M and Guerra Á (2009) High-Frequency coastal upwelling events influence Octopus vulgaris larval dynamics on the NW Iberian shelf. *Marine Ecology Progress Series* 386, 123–132.

Ozturk AA, Dede A, Tonay AM and Ozturk B (2009) Cetacean surveys in the Istanbul (Bosphorus) Strait in 2007-2008. In: Abstracts of 23rd Annual Conf. European Cetacean Society, Istanbul, Turkey.

Paine RT (1980) Food webs: linkage, interaction strength and community infrastructure. *The journal of animal ecology* 49: 666–685.

Palka DL and Hammond PS (2001) Accounting for responsive movement in line transect estimates of abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 777–787.

Palka DL, Rossman MC, VanAtten AS and Orphanides CD (2008) Effect of pingers on harbour porpoise (*Phocoena phocoena*) bycatch in the US Northeast gillnet fishery. *Journal of Cetacean Research and Management* 10(3): 217–226.

Palka, DL (1996) The effect of Beaufort sea state on the sightability of harbour porpoise in the Gulf of Maine. *Report to the International Whaling Commision* 46: 575-582.

Palsbøll PJ, Bérubé M, Larsen AH and Jørgensen H (1997) Primers for the amplification of tri- and tetramer microsatellite loci in baleen whales. *Molecular ecology* 6(9): 893–5.

Panigada S, Pesante G, Zanardelli M, Capoulade F, Gannier A and Weinrich MT (2006) Mediterranean fin whales at risk from fatal ship strikes. *Marine pollution bulletin* 52(10): 1287–98.

Peliz Á, Dubert J, Haidvogel DB and Le Cann B (2003) Generation and unstable evolution of a density-driven Eastern Poleward Current: The Iberian Poleward Current. *Journal of Geophysical Research* 108(C8): 3268.

Peltier H, Baagøe HJ, Camphuysen KCJ, Czeck R, Dabin W, Daniel P, Deaville R, Haelters J, Jauniaux T, Jensen LF, Jepson PD, Keijl GO, Siebert U, Van Canneyt O and Ridoux V (2013) The stranding anomaly as population indicator: the case of harbour porpoise *Phocoena phocoena* in North-Western Europe. *PloS one* 8(4): e62180.

Peltier H, Dabin W, Daniel P, Van Canneyt O, Dorémus G, Huon M and Ridoux V (2012) The significance of stranding data as indicators of cetacean populations at sea: modelling the drift of cetacean carcasses. *Ecological Indicators*. Elsevier Ltd 18: 278–290.

Penas-Patiño XM and Piñeiro A (1989) Cetáceos, focas e tartarugas mariñas das costas Ibéricas. Ed. Consellería de pesca. Xunta de Galicia. Santiago de Compostela. 379 pp.

Pérez T, Vázquez F, Naves J, Fernández A, Corao A, Albornoz J and Domínguez A (2009) Non-invasive genetic study of the endangered Cantabrian brown bear (*Ursus arctos*). *Conservation Genetics* 10(2): 291–301.

Perrin WF, Donovan GP and Barlow J (1994) Gillnets and Cetaceans. Incorporating the proceedings of the symposium and workshop on the mortality of cetaceans in passive fishing nets and traps. *Report of the International Whaling Commission.* Special issue 15.

Pierce GJ, Caldas M, Cedeira J, Santos MB, Llavona Á, Covelo P, Martinez G, Torres J, Sacau M and López A (2010) Trends in cetacean sightings along the Galician coast, north-west Spain, 2003–2007, and inferences about cetacean habitat preferences. *Journal of the Marine Biological Association of the United Kingdom* 90(08): 1547–1560.

Pierce GJ, Santos MB, Murphy S, Learmonth JA, Zuur AF, Rogan E, Bustamante P, Caurant F and Lahaye V (2008) Bioaccumulation of persistent organic pollutants in female common dolphins (*Delphinus delphis*) and harbour porpoises (*Phocoena phocoena*) from western European seas: Geographical trends, causal factors and effects on reproduction and mortality. *Environmental pollution* 153(2): 401–415.

Piertney SB, MacColl a D, Bacon PJ and Dallas JF (1998) Local genetic structure in red grouse (*Lagopus lagopus scoticus*): evidence from microsatellite DNA markers. *Molecular Ecology* 7(12): 1645–54.

Piertney SB, Maccoll ADC, Bacon PJ, Racey PA, Lambin X and Dallas JF (2000) Matrilineal Genetic Structure and Female-Mediated Gene Flow in Red Grouse (*Lagopus lagopus scoticus*): an analysis using mitochondrial DNA. *Evolution* 54(1): 279–289.

Pikesley SK, Witt MJ, Hardy T, Loveridge J, Loveridge J, Williams R and Godley BJ (2011) Cetacean sightings and strandings: evidence for spatial and temporal trends? *Journal of the Marine Biological Association of the United Kingdom* 92: 1809–1820.

Pingree R and Le Cann B (1989) Celtic and Armorican slope and shelf residual currents. *Progress in Oceanography1* 23: 303–338.

Prego R and M Varela (1998) Hidrography of the Artabro Gulf in summer: western coastal limit of Cantabrian seawater and wind-induced upwelling at Prior Cape. *Oceanologica Acta* 21:145-155.

Pritchard JK, Stephens M and Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics* 155:945–959.

Pyenson ND (2010) Carcasses on the coastline: measuring the ecological fidelity of the cetacean stranding record in the eastern North Pacific Ocean. *Paleobiology* 36(3): 453–480.

Pyenson ND (2011) The high fidelity of the cetacean stranding record: insights into measuring diversity by integrating taphonomy and macroecology. *Proceedings of the Royal Society B* (April): 3608–3616.

Read A (2013) REVIEW Development of conservation strategies to mitigate the bycatch of harbor porpoises in the Gulf of Maine. *Endangered Species Research* 20(3): 235–250.

Read AJ (1994) Interactions between cetaceans and gillnet and trap fisheries in the northewest Atlantic. *Report of the International Whaling Commission* (Special issue 15): 133-147.

Read AJ (1999) Harbour porpoise *Phocoena phocoena* (Linnaeus, 1758). In: Handbook of marine mammals. Ridgway SH and Harrison R (eds). Academic Press. Pp.323-350.

Read AJ and Gaskin DE (1985) Radio tracking the movements and activities of harbor porpoises, *Phocoena phocoena*, in the Bay of Fundy. *Fishery Bulletin* 83: 543-552.

Read AJ and Westgate A J (1997) Monitoring the movements of harbour porpoises (*Phocoena phocoena*) with satellite telemetry. *Marine Biology* 130:315-322.

Read AJ, Wiepkema PR and Nachtigall PE (1997) The harbour porpoise (*Phocoena phocoena*). In The biology of the harbour porpoise, AJ Read et al. (eds). Woerden, The Netherlands: De Spil Publishers, 3–6.

Read FL, Santos MB, González ÁF, López A, Ferreira M, Vingada J and Pierce GJ (2012) Understanding harbour porpoise (*Phocoena phocoena*) and fishery interactions in the north-west Iberian Peninsula. Final report to ASCOBANS (SSFA/ASCOBANS/2010/4)

Redfern J, Ferguson M, Becker E, Hyrenbach K, Good C, Barlow J, Kaschner K, Baumgartner M, Forney K, Ballance L, Fauchald P, Halpin P, Hamazaki T, Pershing A, Qian S, Read A, Reilly S, Torres L and Werne F (2006) Techniques for cetacean-–habitat modeling. *Marine Ecology Progress Series* 310: 271–295.

Reed DH and Frankham R (2003) Correlation between fitness and genetic diversity. *Conservation Biology* 17(1): 230–237.

Riccioni G, Ferrara G, Landi M, Sella M, Piccinetti C and Barbujani G (2010) Spatio-temporal genetic patterns in Mediterranean bluefin tuna: populaiton structure and retention of genetic diversity. *Collective Volume of Scientific Papers. ICCAT* 65(3): 996–1003.

Riccioni G, Stagioni M, Landi M, Ferrara G, Barbujani G and Tinti F (2013) Genetic structure of bluefin tuna in the Mediterranean sea correlates with environmental variables. *PloS one* 8(11): e80105.

Richards VP, Greig TW, Fair PA, McCulloch SD, Politz C, Natoli A, Driscoll CA, Hoelzel AR, David V, Bossart GD and Lopez JV (2013) Patterns of population structure for inshore bottlenose dolphins along the Eastern United States. *The Journal of heredity* 104(6): 765–78.

Riffaut L, McCoy K, Tirard C, Friesen V and Boulinier T (2005) Population genetics of the common guillemot, *Uria aalge*, in the North Atlantic: geographic impact of oil spills. *Marine Ecology Progress Series* 291: 263–273.

Ritchie H, Cousins NJ, Cregeen SJ and Piertney SB (2013) Population genetic structure of the abyssal grenadier (*Coryphaenoides armatus*) around the mid-Atlantic ridge. *Deep Sea Research Part II: Topical Studies in Oceanography* 98: 431–437.

Roberge JM and Angelstam P (2004) Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology* 18: 76–85.

Rosel P, Dizon A and Haygood M (1995) Variability of the mitochondril control region in populations of the harbour porpoise, *Phocoena phocoena*, on interoceanic and regional scales. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 1210–1219.

Rosel P, Frantzis A, Lockyer C and Komnenou A (2003) Source of Aegean Sea harbour porpoises. *Marine Ecology Progress Series* 247: 257–261.

Rosel PE, France SC, Wang JY and Kocher TD (1999 b) Genetic structure of harbour porpoise *Phocoena phocoena* populations in the northwest Atlantic based on mitochondrial and nuclear markers. *Molecular ecology* 8 (12 Suppl 1): S41–54.

Rosel PE, Hansen L and Hohn AA (2009) Restricted dispersal in a continuously distributed marine species: common bottlenose dolphins *Tursiops truncatus* in coastal waters of the western North Atlantic. *Molecular Ecology* 18:5030–5045.

Rosel PE, Tiedemann R and Walton M (1999 a) Genetic evidence for limited trans-Atlantic movements of the harbor porpoise *Phocoena phocoena*. *Marine Biology* 133(4): 583–591.

Rosenberg NA (2004) DISTRUCT: a program for the graphical display of population structure. *Molecular Ecology Notes* 4:137–138.

Ross PS (2000) Marine mammals as sentinels in ecological risk assessment. *Human and Ecological Risk Assessment* 6(1): 29–46.

Sala I, Caldeira RMA., Estrada-Allis SN, Froufe E and Couvelard X (2013) Lagrangian transport pathways in the northeast Atlantic and their environmental impact. *Limnology & Oceanography: Fluids & Environments* 3: 40–60.

Santora JA (2012) Habitat use of hourglass dolphins near the South Shetland Islands, Antarctica. *Polar Biology* 35: 801–806.

Santos J, Araújo H, Ferreira M, Henriques A, Miodonski J, Monteiro S, Oliveira I, Rodrigues P, Duro G, Oliveira F, Pinto N, Sequeira M, Eira C and VingadaJ (2012) Chapter I: Baseline estimates of abundance and distribution of target species. Annex to the Midterm Report of project LIFE MarPro PT/NAT/00038.

Santos MB, Pierce GJ, Learmonth JA, Reid RJ, Ross H, Patterson IAM, Reid D and Beare D (2004) Variability in the diet of harbour porpoises (*Phcoena phocoena*) in Scottish waters 1992 – 2003. Marine Mammal Science 20(1): 1–27.

Santos MB and Pierce GJ (2003) The diet of harbour porpoise (*Phocoena phocoena*) in the Northeast Atlantic. *Oceanography and Marine Biology: an Annual Review* 41: 355–390.

Santos MB, Pierce GJ, Ieno EN, Addink M, Smeenk C, Kinze CC and Sacau M (2005) Harbour porpoise (*Phocoena phocoena*) feeding ecology in the eastern North Sea. *ICES CM 2005/THEME SESSION R:15* (Marine Mammals: Monitoring Techniques, Abundance Estimation, and Interactions with Fisheries). 25 pp.

Santos MB, Saavedra C and Pierce GJ (2014) Quantifying the predation on sardine and hake by cetaceans in the Atlantic waters of the Iberian Peninsula. *Deep Sea Research Part II: Topical Studies in Oceanography* 106: 232–244.

Scheidat M, Castro C, Gonzalez J and Williams R (2004) Behavioural responses of humpback whales (*Megaptera novaeangliae*) to whalewatching boats near Isla de la Plata, Machalilla National Park, Ecuador. *Journal of Cetacean Research and Management* 6(1): 1–6.

Scheidat M, Gilles A, Kock KH and Siebert U (2008) Harbour porpoise *Phocoena phocoena* abundance in the southwestern Baltic Sea. *Endangered Species Research* 5 (December): 215–223.

Scheidat M, Tougaard J, Brasseur S, Carstensen J, Petel TVP and Teilmann J (2011) Harbour porpoises (*Phocoena phocoena*) and wind farms: a case study in the Dutch North Sea. *Environmental Research Letters* 025102(6): 10.

Scheidat M, Verdaat H and Aarts G (2012) Using aerial surveys to estimate density and distribution of harbour porpoises in Dutch waters. *Journal of Sea Research*. 69: 1–7.

Schumann N, Gales N, Harcourt R and Arnould J (2013) Impacts of climate change on Australian marine mammals. *Australian Journal of Zoology*. 61(2): 146–159.

Schwartz MK, Luikart G and Waples RS (2007) Genetic monitoring as a promising tool for conservation and management. *Trends in ecology & evolution* 22(1): 25–33.

Sequeira M (1996) Harbour porpoises (*Phocoena phocoena*) in Portuguese waters. *Report of the International Whaling Commission* 46: 583-586.

Sequeira M and Inácio A (1992) Accidental catches of cetaceans in Portugal. *European Research on Cetaceans* 6: 25-28.

Sequeira M, Inácio A and Reiner F (1992) Arrojamentos de Mamíferos Marinhos na Costa Portuguesa entre 1978 e 1988. Estudos de Biología e Conservaçao da Natureza 7. Servicio Nacional de Parques, Reservas e Conservaçao da Natureza, Lisboa. 48 pp.

Sequeira M, Inácio A, Silva MA and Reiner F (1996) Arrojamentos de Mamíferos Marinhos na Costa Continental Portuguesa entre 1989-1994. Estudos de Biología e Conservaçao da Natureza 19. Servicio Nacional de Parques, Reservas e Conservaçao da Natureza. Lisboa. 52 pp

Sergio F, Caro T, Brown D, Clucas B, Hunter J, Ketchum J, McHugh K and Hiraldo F (2008) Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Annual Review of Ecology, Evolution, and Systematics* 39: 1–19.

Sergio F, Newton I, Marchesi L and Pedrini P (2006) Ecologically justified charisma: Preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology* 43: 1049–1055.

Shucksmith R, Jones NH, Stoyle GW, Davies A and Dicks EF (2008) Abundance and distribution of the harbour porpoise (*Phocoena phocoena*) on the north coast of Anglesey, Wales, UK. *Journal of the Marine Biological Association of the United Kingdom* 89(05): 1051.

Siebert U, Gilles A, Lucke K, Ludwig M, Benke H, Kock K-H and Scheidat M (2006) A decade of harbour porpoise occurrence in German waters—Analyses of aerial surveys, incidental sightings and strandings. *Journal of Sea Research* 56(1): 65–80.

Siebert U, Joiris C, Holsbeek L, Benke H, Failing K, Frese K and Petzinger E (1999) Potetial relation between mercury concentrations and necropsy findings in cetaceans from German waters of North and Baltic seas. *Marine pollution bulletin* 38(4): 285–295.

Siebert U, Wünschmann A, Weiss R, Frank H, Benke H and Frese K (2001) Post-mortem findings in harbour porpoises (*Phocoena phocoena*) from the German North and Baltic Seas. *Journal of comparative pathology* 124(2-3): 102–14.

Silva MA, Prieto R, Cascão I, Seabra MI, Machete M, Baumgartner MF and Santos RS (2014) Spatial and temporal distribution of cetaceans in the mid-Atlantic waters around the Azores. *Marine Biology Research* 10(2): 123–137.

Silva MA, Sequeira M, Prieto R and Alexandre B (1999) Observations of harbour porpoises (*Phocoena phocoena*) in the Northern coast of Portugal. In: European Research on Cetaceans, nº13. Evans PGH, Cruz J and Raga, JA eds: 267-269. *Proceedings of the 13th Annual Conference of the European Cetacean Society*. Valencia, Spain.

Simberloff D (1988) The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics* 19: 473–511.

Simmonds MP and Lopez-Jurado LF (1991) Whales and the military. *Nature* 351: 448.

Simon M, Nuuttila H, Reyes-Zamudio MM, Ugarte F, Verfub U and Evans PGH (2010) Passive acoustic monitoring of bottlenose dolphin and harbour porpoise, in Cardigan Bay, Wales, with implications for habitat use and partitioning. *Journal of the Marine Biological Association of the United Kingdom* 90(08): 1539–1545.

Skov H and Thomsen F (2008) Resolving fine-scale spatio-temporal dynamics in the harbour porpoise *Phocoena phocoena*. *Marine Ecology Progress Series* 373: 173–186.

Skove S, Durnick J and Bloch D (2003) Habitat characteristics of the shelf distribution of the harbour porpoise (*Phocoena phocoena*) in the waters around the Faroe Islands during summer. In: Haug T, Desportes G, Vikingsson G, Witting L (eds). Harbour porpoises in the North Atlantic. *NAMMCO Sci. Publ.* 5: 31-40.

Smith-Vaniz WF (1986) Carangidae. p. 815-844. In P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese (eds.) Fishes of the north-eastern Atlantic and the Mediterranean. UNESCO, Paris. vol. 2.

Sorensen TB and Kinze CC (1994) Reproduction and reproductive seasonality in Danish harbour porpoises, *Phocoena phocoena*. *Ophelia1* 39(3): 159–176.

Spanish Ministry of Agriculture and Envrionment, (2013) www.magrama.gob.es/es/estadistica/temas/estadisticas-pesqueras/Estadisticas_Pesqueras_2013-11_tcm7-309328.PDF)

Spitz J, Rousseau Y and Ridoux V (2006) Diet overlap between harbour porpoise and bottlenose dolphin: an argument in favour of interference competition for food? *Estuarine, Coastal and Shelf Science* 70(October): 259–270.

Spyrakos E, Santos-Diniz TC, Martinez-Iglesias G, Torres-Palenzuela JM and Pierce GJ (2011) Spatiotemporal patterns of marine mammal distribution in coastal waters of Galicia, NW Spain. *Hydrobiologia* 670(1): 87–109.

Stenson G (2003) Harbour porpoise (*Phocoena phocoena*) in the North Atlantic: Abundance, removals, and sustainability of removals. In: Haug T, Desportes G, Vikingsson G, Witting L (eds). Harbour porpoises in the North Atlantic. *NAMMCO Sci Pub*, Vol. 5. 271–302.

Stockin KA, Amaral AR, Latimer J, Lambert DM and Natoli A (2013) Population genetic structure and taxonomy of the common dolphin (Delphinus sp.) at its southernmost range limit: New Zealand waters. *Marine Mammal Science* 30(1): 44–63.

Sveegaard S, Teilmann J, Tougaard J, Dietz R, Mouritsen KN, Desportes G and Siebert U (2011) High-density areas for harbor porpoises (*Phocoena phocoena*) identified by satellite tracking. *Marine Mammal Science* 27(1): 230–246.

Sveegaard S, Galatius A, Dietz R, Kyhn L, Koblitz JC, Amundin M, Nabe-Nielsen J, Sinding M-H S, Andersen LW and Teilmann J (2015) Defining management units for cetaceans by combining genetics, morphology, acoustics and satellite tracking. *Global Ecology and Conservation* 3: 839–850.

Svetovidov AN (1986) Gadidae. p. 680-710. In PJP Whitehead, M-L Bauchot, J-C Hureau, J Nielsen and E Tortonese (eds.) Fishes of the north-eastern Atlantic and the Mediterranean. UNESCO, Paris. vol. 2.

Swenson JE, Taberlet P and Bellemain E (2011) Genetics and conservation of European brown bears *Ursus arctos*. *Mammal Review* 41(2): 87–98.

Taberlet P, Fumagalli L, Wust-Saucy A-G and Cosson J-F (1998) Comparative phylogeography and postglacial colonization. *Molecular Ecology* 7: 453–464.

Tallmon DA, Luikart G and Waples RS (2004) The alluring simplicity and complex reality of genetic rescue. *Trends in ecology & evolution* 19(9): 489–96.

Tamura K, Dudley J, Nei M and Kumar S (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution* 24(8): 1596–1599.

Taylor B and Dizon A (1999) First policy then science : why a management unit based solely on genetic criteria cannot work. *Molecular Ecology* 8: 11–16.

Teilmann J and Carstensen J (2012) Negative long term effects on harbour porpoises from a large scale offshore wind farm in the Baltic—evidence of slow recovery. *Environmental Research Letters* 7(4): 045101.

Teilmann J and Dietz R (1998) Status of the harbour porpoise in Greenland. *Polar Biology* 19: 211–220.

Teske PR, Cherry MI and Matthee CA (2003) Population genetics of the endangered Knysna seahorse, *Hippocampus capensis*. *Molecular Ecology* 12(7): 1703–1715.

Thangaraj M, Lipton AP and Gopalakrishnan A (2012) Genetic diversity of three spotted seahorse, *Hippocampus trimaculatus* (Leach, 1814) in India using four microsatellite loci. *Notulae Scientia Biologicae* 4(4): 7–13.

Thomsen F, Laczny M and Piper W (2006) A recovery of harbour porpoises (*Phocoena phocoena*) in the southern North Sea? A case study off Eastern Frisia, Germany. *Helgoland Marine Research* 60(3): 189–195.

Tiedemann R, Harder J, Gmeiner C and Haase E (1996) Mitochondrial DNA sequence patterns of harbour porpoises (*Phocoena phocoena*) from the North and the Baltic Sea. *Z. Säugetierkunde* 61: 104–11.

Tolley K and Rosel P (2006) Population structure and historical demography of eastern North Atlantic harbour porpoises inferred through mtDNA sequences. *Marine Ecology Progress Series* 327: 297–308.

Tolley KA, Rosel PE, Walton W, Bjørje A and Øien N (1999) Genetic population structure of harbour porpoise (*Phocoena phocoena*) in the North Sea and Norwegian waters. *Journal of Cetacean Research and Management* 1(3): 265-274.

Tolley KA, Vikingsson GA and Rosel PE (2001) Mitochondrial DNA sequence variation and phylogeographic patterns in harbour porpoises (*Phocoena phocoena*) from the North Atlantic. *Conservation Genetics* 3: 349–361.

Tonay AM and Dede A (2013) First stranding record of a harbour porpoise (*Phocoena phocoena*) in the Southern Aegean Sea. *Journal of Black Sea/Mediterranean Envrionment* 19(1): 132–137.

Tonay AM, Dede A, Maracı Ö and Bilgin R (2012) A preliminary genetic study on the harbour porpoise (*Phocoena phocoena*) in the Turkish Seas. *Journal of the Black Sea / Mediterranean Environment* 18(1): 83–89.

Tonay AM, Dede A, Öztürk AA and Öztürk B (2007) Stomach content of harbour poroises (*Phocoena phocoena*) from the Turkish western Black sea in spring and early summer. R*apports du Commission Intérnationale Mer Méditerranée* 38: 616.

Tonay AM, Dede A, Ozturk AA and Ozturk B (2009) Cetacean strandings in the Turkish Straits System (TSS) and the Northern Aegean Sea coast of Turkey during 1999-2008. Proceedings of the 23rd Annual Conference of the European Cetacean Society. Istanbul, Turkey.

Torres R, Barton ED, Miller P and Fanjul E (2003) Spatial patterns of wind and sea surface temperature in the Galician upwelling region. *Journal of Geophysical Research 108: 3130*. doi:10.1029/2002JC001361

Torres R and Barton ED (2007) Onset of the Iberian upwelling along the Galician coast. *Continental Shelf Research* 27(13): 1759–1778.

Tougaard J, Henriksen OD and Miller LA (2009) Underwater noise from three types of offshore wind turbines: estimation of impact zones for harbor porpoises and harbor seals. *Acoustical Society of America* 125(6): 3766–3773.

Triñanes JA, Cotos JM, Torres J and Arias J (1993) Mapas SST de alta resolución mediante combinación de datos TM-AVHRR. *Revista de teledeteccion* 2: 1–8.

Trippel EA, Holy NL and Shepherd TD (2008) Barium sulphate modified fishing gear as a mitigative measure for cetacean incidental mortalities. *Journal of Cetacean Research and Management* 10(3): 235–246.

Trippel EA, Holy NL, Palka DL, Shepherd TD, Melvin GD and Terhune JM (2003) Nylon barium sulphate gillnet reduces porpoise and seabird mortality. *Marine Mammal Sci*ence 19: 240-43.

Trites AW, Miller AJ, Maschner HDG, Alexander M a., Bograd SJ, Calder J a., Capotondi A, Coyle KO, Lorenzo E Di, Finney BP, Gregr EJ, Grosch CE, Hare SR, Hunt GL, Jahncke J, Kachel NB, Kim HJ, Ladd C, Mantua NJ, Marzban C, Maslowski W, Mendelssohn R, Neilson DJ, Okkonen SR, Overland JE, Reedy-Maschner KL, Royer TC, Schwing FB, Wang JXL and Winship AJ (2007) Bottom-up forcing and the decline of Steller sea lions (*Eumetopias jubatas*) in Alaska: Assessing the ocean climate hypothesis. *Fisheries Oceanography* 16(1): 46–67.

Truchon M-H, Measures L, L'Hérault V, Brêthes J-C, Galbraith PS, Harvey M, Lessard S, Starr M and Lecomte N (2013) Marine mammal strandings and environmental changes: a 15-year study in the St. Lawrence ecosystem. *PloS one* 8(3): e59311.

Tynan CT, Ainley DG, Barth JA., Cowles TJ, Pierce SD and Spear LB (2005) Cetacean distributions relative to ocean processes in the northern California Current System. *Deep Sea Research Part II: Topical Studies in Oceanography* 52(1-2): 145–167.

Underwood EJ (1977) Trace elements in human and animal nutrition. New York: Academic Press.

Valsecchi E and Amos W (1996) Microsatellite markers for the study of cetacean populations. *Molecular ecology* 5(1): 151–6.

van Oosterhout C, Hutchinson WF, Wills DP, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes* 4: 535–538.

van Waerebeek K (2007) Conservation status of the Northwest African population of the harbour porpoise. *14th Meeting of the CMS Scientific Council*. Bonn, Germany, 14-17 March. Pp 10. CMS/ScC14/Doc.7.

Verfuß UK, Honnef CG, Meding A, Dahne M, Mundry R and Benke H (2007) Geographical and seasonal variation of harbour porpoise (*Phocoena phocoena*) presence in the German Baltic Sea revealed by passive acoustic monitoring. *Journal of the Marine Biological Association of the United Kingdom* 8, 165–176.

Viaud-Martínez KA, Vergara MM, Gol'din PE, Ridoux V, Öztürk AA, Öztürk B, Rosel PE, Frantzis A, Komnenou A and Bohonak AJ (2007) Morphological and genetic differentiation of the Black Sea harbour porpoise *Phocoena phocoena*. *Marine Ecology Progress Series* 338: 281–294.

Víkingsson GA, Elvarsson BÞ, Ólafsdóttir D, Sigurjónsson J, Chosson V and Galan A (2014) Recent changes in the diet composition of common minke whales (*Balaenoptera*

acutorostrata) in Icelandic waters. A consequence of climate change? *Marine Biology Research* 10(2): 138–152.

Víkingsson GA, Ólafsdóttir D and Sigurjónsson J (2003) Diet of harbour porpoises (*Phocoena phocoena*) in Icelandic coastal waters. NAMMCO Sci. Publ. 5:243-270.

VV.AA. (2012) Estrategias marinas: evaluación inicial, buen estado ambiental y objetivos ambientales. Ministerio de Agricultura, Alimentación y Medio Ambiente. 445 pp.

Walton MJ (1997) Population structure of harbour porpoises *Phocoena phocoena* in the seas around the UK and adjacent waters. *Proceedings of the Royal Society B* 264(1378): 89–94.

Wang JY and Berggren P (1997) Mitochondrial DNA analysis of harbour porpoises (*Phocoena phocoena*) in the Baltic Sea, the Kattegat-Skagerrak Seas and off the west coast of Norway. *Marine Biology* 127(4): 531–537.

Wang JY, Gaskin DE and White BN (1996) Mitochondrial DNA analysis of the harbour porpoise, (*Phocoena phocoena*), subpopulations in North American waters. *Canadian Journal of Fisheries and Aquatic Sciences* 53(7): 1632–1645.

Wang K, Wang D, Zhang X, Pfluger A and Barrett L (2006) Range-wide Yangtze freshwater dolphin expedition: the last chance to see Baiji? *Conservation Biology* 13(6): 418–424.

Weijs L, van Elk C, Das K, Blust R and Covaci A (2010) Persistent organic pollutants and methoxylated PBDEs in harbour porpoises from the North Sea from 1990 until 2008: Young wildlife at risk? *The Science of the total environment* 409(1): 228–37.

Weilgart LS (2007) The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Canadian Journal of Zoology* 85(11): 1091–1116.

Weir B and Cockerham CC (1984) Estimating f-statistics for the analysis of population structure. *Evolution* 38(6):1358–1370.

Weir CR, Stockin KA and Pierce GJ (2007) Spatial and temporal trends in the distribution of harbour porpoises, white-beaked dolphins and minke whales off Aberdeenshire (UK), north-western North Sea. *Journal of the Marine Biological Association of the UK* 87(01): 327.

Wenzel MA, Webster LMI, Blanco G, Burgess MD, Kerbiriou C, Segelbacher G, Piertney SB and Reid JM (2012) Pronounced genetic structure and low genetic diversity in European red-billed chough (*Pyrrhocorax pyrrhocorax*) populations. *Conservation Genetics* 13(5): 1213–1230.

Westgate AJ, Read AJ, Berggen P, Koopman HN and Gaskin DE (1995) Diving behaviour of harbour porpoises, *Phocoena phocoena. Canadian Journal of Fisheries and Aquatic Sciences* 52: 1064-1073.

Whitehead PJP (1985) FAO species catalogue. Vol. 7. Clupeoid fishes of the world. An annotated and illustrated catalogue of the herrlngs, sardines, pilchards, sprats, anchovies and wolf-herrlngs. Part I - Chirocentridae, Clupeidae and Pristigasteridae. *FAO Fisheries Synopsis* 125(7) Part 1. 303 pp.

Wiemann A, Andersen LW, Berggren P, Siebert U, Benke H, Teilmann J, Lockyer C, Pawliczka I, Skóra K, Roos A, Lyrholm T, Paulus KB, Ketmaier V and Tiedemann R (2010) Mitochondrial Control Region and microsatellite analyses on harbour porpoise (*Phocoena phocoena*) unravel population differentiation in the Baltic Sea and adjacent waters. *Conservation Genetics* 11(1): 195–211.

Williams R, Bain D, Ford J and Trites A (2002 a) Behavioural responses of male killer whales to a 'leapfrogging' vessel. *Journal of Cetacean Research and Management* 4(3): 305–310.

Williams R, Trites AW and Bain DE (2002 b) Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. *Journal of Zoology* 256(2): 255–270.

Williams TM, Estes J A, Doak DF and Springer AM (2004) Killer appetites: Assessing the role of predators in ecological communities. *Ecology* 85(12): 3373–3384.

Wright S (1951) The genetical structure of populations. *Annals of Eugenics* 15(4):323–354.

Yasui, WY, Gaskin DE (1986) Energy budget of a small cetacean: the harbour porpoise *Phocoena phocoena* L. *Ophelia* 25: 183–198.

Yurik DB and Gaskin DE (1987) Morphometric and meristic comparison of skulls of harbour porpoises *Phocoena phocena* (L.) from the North Atlantic and North Pacific. *Ophelia* 27: 53-75.

Zacharias MA and Roff JC (2001) Use of focal species in marine conservation and management: a review and critique. *Aquatic Conservation: Marine and Freshwater Ecosystems* 11: 59–76.

Zuur AF, Ieno EN and Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1(1): 3–14.

Zuur AF, Ieno EN and Smith GM (2007) Analysing ecological data. Statistics for Biology and Health. Springer New York. 672 pp.

SUPPLEMENTARY MATERIAL

Appendix I. Allele frequencies for the 10 microsatellite loci used in this study.

Population		PORT	GAL	FRA	BELG	IREL	ENG	SCOT	TUR	BCO	HUEL	Group 1	Group 2	Group 3
PPH137	N	104	59	22	13	20	24	23	13	2	2	108	102	13
	Allele													
	98	0	0	0.091	0	0	0	0	0	0	0	0.000	0.020	0.000
	100	0.019	0	0	0.038	0.075	0	0	0.038	0	0	0.012	0.020	0.038
	102	0.005	0.034	0.114	0.077	0	0.042	0.109	0	0	0	0.015	0.068	0.000
	104	0.014	0.008	0	0	0.025	0	0.043	0	0.500	0	0.018	0.015	0.000
	106	0.413	0.229	0.205	0.192	0.125	0.125	0.261	0.154	0	0.500	0.343	0.181	0.154
	108	0.014	0.068	0.023	0	0.025	0.063	0.065	0	0	0	0.033	0.039	0.000
	110	0.173	0.22	0.114	0.077	0.125	0.167	0.065	0	0	0	0.187	0.113	0.000
	112	0.048	0.042	0.091	0.154	0.125	0.063	0.043	0.077	0.500	0	0.051	0.088	0.077
	114	0.115	0.144	0.114	0.077	0.175	0.188	0.174	0.538	0	0	0.123	0.152	0.538
	116	0.053	0.102	0.114	0.231	0.1	0.229	0.087	0.192	0	0	0.069	0.147	0.192
	118	0.125	0.127	0.091	0	0.15	0.104	0.043	0	0	0.500	0.126	0.083	0.000
	120	0.01	0.008	0.045	0.115	0.025	0	0.065	0	0	0	0.009	0.044	0.000
	122	0.01	0.017	0	0.038	0.05	0.021	0.043	0	0	0	0.012	0.029	0.000

Appendix I. Continued.

Population		PORT	GAL	FRA	BELG	IREL	ENG	SCOT	TUR	BCO	HUEL	Group 1	Group 2	Group 3
415/416	N	114	59	17	13	19	24	18	10	2	1	117	91	10
	Allele													
	205	0.004	0	0	0	0	0	0	0	0	0	0.003	0.000	0.000
	209	0	0	0	0.038	0	0.021	0	0	0	0	0.000	0.011	0.000
	211	0	0.008	0	0	0	0.021	0	0.050	0	0	0.003	0.005	0.050
	215	0.754	0.771	0.647	0.692	0.632	0.563	0.639	0.600	0.500	0.500	0.756	0.626	0.600
	217	0.228	0.195	0.176	0.231	0.289	0.396	0.306	0.350	0.500	0	0.219	0.291	0.350
	219	0.004	0.008	0.059	0.038	0.053	0	0.056	0	0	0.500	0.008	0.038	0.000
	221	0	0.017	0	0	0.026	0	0	0	0	0	0.006	0.005	0.000
	231	0.004	0	0	0	0	0	0	0	0	0	0.003	0.000	0.000
	237	0.004	0	0	0	0	0	0	0	0	0	0.003	0.000	0.000
	283	0	0	0.118	0	0	0	0	0	0	0	0.000	0.022	0.000

Appendix I. Continued.

Population		PORT	GAL	FRA	BELG	IREL	ENG	SCOT	TUR	BCO	HUEL	Group 1	Group 2	Group 3
PPH130	N	116	57	24	12	17	24	25	14	2	2			
	Allele													
	158	0	0	0.021	0	0	0	0	0	0	0	0.000	0.005	0.000
	170	0	0	0	0	0	0.021	0	0	0	0	0.000	0.005	0.000
	172	0.022	0.009	0.042	0	0.029	0.083	0.02	0	0	0	0.017	0.040	0.000
	174	0.047	0.009	0	0	0.059	0.063	0.04	0.036	0	0	0.034	0.040	0.036
	176	0.504	0.632	0.375	0.292	0.353	0.250	0.16	0.464	1	0.750	0.554	0.282	0.464
	178	0.004	0.018	0.083	0.125	0.118	0.104	0.200	0.250	0	0.250	0.011	0.124	0.250
	180	0.004	0.018	0.083	0.125	0.029	0.042	0.06	0	0	0	0.008	0.064	0.000
	182	0.155	0.140	0.083	0.125	0.147	0.042	0.18	0	0	0	0.147	0.114	0.000
	184	0.004	0	0.083	0.125	0	0.021	0.1	0	0	0	0.003	0.059	0.000
	186	0.043	0.026	0.104	0.042	0.029	0.063	0.12	0	0	0	0.037	0.079	0.000
	188	0.017	0	0.021	0.042	0.029	0.146	0.04	0.214	0	0	0.011	0.059	0.214
	190	0	0.018	0.104	0.083	0.147	0.063	0.04	0.036	0	0	0.006	0.084	0.036
	192	0	0	0	0	0	0.021	0.02	0	0	0	0.000	0.010	0.000
	194	0.017	0.018	0	0.042	0.059	0	0.02	0	0	0	0.017	0.020	0.000
	196	0.039	0.009	0	0	0	0.042	0	0	0	0	0.028	0.010	0.000
	198	0.142	0.105	0	0	0	0.042	0	0	0	0	0.127	0.010	0.000

Appendix I. Continued.

Population		PORT	GAL	FRA	BELG	IREL	ENG	SCOT	TUR	BCO	HUEL	Group 1	Group 2	Group 3
PPH110	N	116	59	23	15	22	24	25	16	2	2	120	109	16
	Allele													
	99	0	0	0	0	0	0.021	0	0	0	0	0.000	0.005	0.000
	101	0	0	0.022	0.033	0.045	0.042	0	0	0	0	0.000	0.028	0.000
	107	0	0	0.022	0.033	0.023	0	0	0	0	0	0.000	0.014	0.000
	109	0.310	0.356	0.174	0.167	0.091	0.146	0.080	0.031	0.500	0	0.324	0.130	0.031
	111	0.009	0.008	0.065	0.100	0.045	0.021	0.040	0.031	0	0	0.008	0.051	0.031
	113	0.034	0.076	0.087	0.133	0.091	0.083	0.180	0.500	0	0.500	0.053	0.116	0.500
	115	0.384	0.364	0.174	0.133	0.273	0.292	0.200	0	0	0.500	0.374	0.222	0.000
	117	0.254	0.186	0.326	0.200	0.273	0.208	0.280	0.438	0.500	0	0.232	0.259	0.437
	119	0.004	0	0.130	0.167	0.091	0.146	0.220	0	0	0	0.003	0.148	0.000
	121	0	0	0	0.033	0.068	0.042	0	0	0	0	0.000	0.028	0.000
	125	0.004	0.008	0	0	0	0	0	0	0	0	0.006	0.000	0.000

Appendix I. Continued.

Population		PORT	GAL	FRA	BELG	IREL	ENG	SCOT	TUR	BCO	HUEL	Group 1	Group 2	Group 3
GT011	N	117	57	23	14	22	24	25	15	2	2	121	108	15
	Allele													
	96	0	0	0	0	0	0	0.020	0	0	0	0.000	0.005	0.000
	106	0	0.009	0.022	0	0	0	0.020	0	0	0	0.003	0.009	0.000
	108	0.756	0.781	0.457	0.250	0.318	0.313	0.360	0.200	0	0.750	0.756	0.346	0.200
	110	0.209	0.114	0.217	0.250	0.295	0.167	0.120	0.700	0.500	0.250	0.183	0.206	0.700
	111	0	0	0.043	0	0	0.021	0.020	0.033	0.250	0	0.003	0.019	0.033
	112	0.026	0.035	0.065	0.036	0	0	0.020	0.033	0	0	0.028	0.019	0.033
	114	0	0.009	0	0.036	0.023	0.021	0	0.033	0	0	0.003	0.014	0.033
	118	0	0	0.043	0.036	0.045	0.042	0	0	0	0	0.000	0.033	0.000
	120	0	0	0	0.107	0.068	0.104	0.080	0	0	0	0.000	0.070	0.000
	122	0.004	0.026	0.043	0.036	0.045	0.042	0.060	0	0	0	0.011	0.046	0.000
	124	0.004	0.018	0.043	0.107	0.091	0.104	0.140	0	0	0	0.008	0.098	0.000
	126	0	0.009	0	0.107	0.068	0.167	0.100	0	0.250	0	0.006	0.089	0.000
	128	0	0	0.065	0.036	0.045	0	0.060	0	0	0	0.000	0.042	0.000
	132	0	0	0	0	0	0.021	0	0	0	0	0.000	0.005	0.000

Appendix I. Continued.

Population		PORT	GAL	FRA	BELG	IREL	ENG	SCOT	TUR	BCO	HUEL	Group 1	Group 2	Group 3
EV94	N	114	59	20	8	19	20	18	13	2	2	118	85	13
	Allele													
	184	0	0	0	0	0	0	0.028	0	0	0	0.000	0.006	0.000
	190	0.004	0	0	0	0	0	0.028	0	0	0	0.003	0.006	0.000
	192	0.004	0	0	0	0	0	0	0.038	0	0	0.003	0.000	0.038
	194	0.474	0.373	0.350	0.188	0.368	0.150	0.111	0.654	0	0.500	0.435	0.241	0.654
	196	0.004	0.059	0.075	0	0.053	0	0.139	0.115	0.250	0	0.025	0.060	0.115
	198	0.303	0.364	0.200	0.438	0.289	0.325	0	0	0	0.500	0.322	0.229	0.000
	200	0.140	0.169	0.100	0.313	0.053	0.225	0.333	0.154	0.500	0	0.152	0.188	0.154
	202	0.061	0.025	0.125	0	0.158	0.075	0.222	0.038	0	0	0.048	0.129	0.038
	204	0.009	0.008	0.125	0.063	0.079	0.150	0.139	0	0.250	0	0.011	0.118	0.000
	206	0	0	0.025	0	0	0.075	0	0	0	0	0.000	0.023	0.000
	149	0.005	0.009	0.022	0.125	0.023	0	0	0.133	0	0.250	0.009	0.028	0.133
	151	0	0	0	0	0.023	0.022	0	0.300	0	0	0.000	0.009	0.300
	153	0.009	0.018	0	0	0	0	0	0.033	0	0	0.012	0.000	0.033

Appendix I. Continued.

Population		PORT	GAL	FRA	BELG	IREL	ENG	SCOT	TUR	BCO	HUEL	Group 1	Group 2	Group 3
Igf-I	N	106	56	23	16	22	23	24	15	2	2	110	108	15
	Allele													
	127	0	0.009	0	0	0	0.065	0	0	0	0	0.003	0.014	0.000
	129	0	0	0	0.031	0	0	0	0	0	0	0.000	0.005	0.000
	131	0	0.009	0	0	0.023	0.022	0.083	0	0	0	0.003	0.028	0.000
	133	0.005	0	0.065	0	0.091	0.043	0.146	0	0	0	0.003	0.075	0.000
	135	0.019	0.009	0.065	0.063	0.091	0.196	0.146	0	0	0	0.015	0.117	0.000
	137	0.057	0.045	0.196	0.125	0.159	0.174	0.229	0.400	0	0.250	0.054	0.182	0.400
	139	0.774	0.732	0.304	0.219	0.250	0.130	0.146	0.033	0	0.250	0.744	0.206	0.033
	141	0.094	0.107	0.130	0.125	0.091	0.152	0.104	0	0.500	0	0.102	0.117	0.000
	143	0.009	0.027	0.130	0.063	0.091	0.087	0.063	0	0.250	0	0.018	0.089	0.000
	144	0	0	0	0	0.023	0.022	0	0	0	0	0.000	0.009	0.000
	145	0.028	0.027	0.043	0.063	0.114	0.043	0.021	0.033	0.250	0.250	0.033	0.056	0.033
	147	0	0.009	0.043	0.188	0.023	0.043	0.063	0.067	0	0	0.003	0.065	0.067

Appendix I. Continued.

Population		PORT	GAL	FRA	BELG	IREL	ENG	SCOT	TUR	BCO	HUEL	Group 1	Group 2	Group 3
PPH104	N	113	59	23	16	24	24	25	16	2	2	117	112	16
	142	0	0	0	0	0	0.042	0	0	0	0	0.000	0.009	0.000
	144	0.004	0	0	0	0	0	0	0	0	0	0.003	0.000	0.000
	150	0.004	0	0.022	0.031	0	0.021	0.020	0	0	0	0.003	0.018	0.000
	152	0	0	0.043	0	0.021	0	0	0	0	0	0.000	0.013	0.000
	154	0	0	0.022	0	0	0	0.020	0	0	0	0.000	0.009	0.000
	156	0	0.008	0.022	0.063	0.042	0.042	0.040	0	0	0	0.003	0.040	0.000
	158	0.133	0.085	0.109	0.125	0	0.208	0.140	0.031	0.250	0.250	0.119	0.117	0.031
	160	0.062	0.110	0.087	0.125	0.125	0.167	0.120	0	0	0	0.077	0.126	0.000
	162	0.062	0.102	0.065	0.250	0.229	0.167	0.060	0.531	0.500	0.250	0.082	0.149	0.531
	164	0.376	0.314	0.196	0.125	0.313	0.167	0.160	0.063	0.250	0	0.349	0.198	0.062
	166	0.119	0.161	0.261	0.063	0.125	0.063	0.200	0	0	0	0.131	0.144	0.000
	168	0.119	0.076	0.065	0.063	0.042	0.063	0.100	0.156	0	0	0.102	0.068	0.156
	170	0.106	0.119	0.043	0.063	0.063	0.063	0.120	0.063	0	0	0.108	0.072	0.062
	172	0	0.008	0.022	0.063	0	0	0	0.125	0	0	0.003	0.009	0.125
	174	0.009	0.017	0.022	0	0.042	0	0.020	0.031	0	0.250	0.014	0.018	0.031
	176	0	0	0.022	0.031	0	0	0	0	0	0	0.000	0.009	0.000
	184	0.004	0	0	0	0	0	0	0	0	0	0.003	0.000	0.000
	188	0	0	0	0	0	0	0	0	0	0.250	0.003	0.000	0.000

Appendix I. Continued.

Population		PORT	GAL	FRA	BELG	IREL	ENG	SCOT	TUR	BCO	HUEL	Group 1	Group 2	Group 3
GT015	N	105	52	22	12	20	21	20	13	2	2	109	95	13
	Allele													
	120	0.005	0	0	0	0	0	0	0	0	0	0.003	0.000	0.000
	122	0.048	0.038	0	0	0	0	0	0	0	0	0.043	0.000	0.000
	130	0	0	0	0	0.025	0.024	0.050	0	0	0	0.000	0.021	0.000
	132	0.138	0.087	0.023	0.042	0	0.048	0.200	0	0	0	0.118	0.063	0.000
	134	0.062	0.038	0.136	0.208	0	0.119	0.025	0	0.250	0.250	0.059	0.089	0.000
	136	0.076	0.077	0.159	0.125	0.225	0.238	0.125	0.769	0	0.500	0.081	0.179	0.769
	138	0.090	0.077	0.091	0.083	0.025	0.024	0.025	0.077	0	0	0.084	0.047	0.077
	140	0.005	0.038	0.045	0	0	0	0.025	0.038	0	0	0.015	0.016	0.038
	142	0	0	0	0.083	0	0	0.075	0	0	0	0.000	0.026	0.000
	144	0	0.029	0	0	0	0.024	0	0	0	0	0.009	0.005	0.000
	146	0.052	0.048	0.045	0.042	0.025	0.024	0.075	0	0	0	0.050	0.042	0.000
	148	0.071	0.096	0.045	0	0	0.024	0	0	0.250	0	0.081	0.016	0.000
	150	0.124	0.144	0.136	0	0.050	0.095	0.025	0	0	0.250	0.130	0.068	0.000
	152	0.024	0.058	0.205	0	0.075	0.048	0.025	0.115	0	0	0.034	0.079	0.115
	154	0	0.010	0.045	0.042	0.075	0.071	0.025	0	0	0	0.003	0.053	0.000
	156	0.052	0.029	0	0.042	0.075	0	0.050	0	0	0	0.043	0.032	0.000
	158	0.095	0.087	0.023	0	0.025	0.024	0.075	0	0	0	0.090	0.032	0.000
	160	0.014	0	0	0	0.075	0	0.025	0	0.250	0	0.012	0.021	0.000
	162	0.038	0.019	0	0.125	0.100	0	0.075	0	0.250	0	0.034	0.053	0.000
	164	0.014	0.019	0	0.042	0.150	0.071	0.050	0	0	0	0.015	0.063	0.000
	166	0.062	0.048	0	0.083	0.025	0.095	0.050	0	0	0	0.056	0.047	0.000
	168	0.014	0.038	0.023	0.083	0.025	0.071	0	0	0	0	0.022	0.037	0.000
	170	0.010	0.010	0.023	0	0.025	0	0	0	0	0	0.009	0.010	0.000

Appendix I. Continued.

Population		PORT	GAL	FRA	BELG	IREL	ENG	SCOT	TUR	BCO	HUEL	Group 1	Group 2	Group 3
GT015	N	105	52	22	12	20	21	20	13	2	2	109	95	13
	Allele													
	172	0.005	0.010	0	0	0	0	0	0	0	0	0.006	0.001	0.000

Appendix I. Continued.

Population		PORT	GAL	FRA	BELG	IREL	ENG	SCOT	TUR	BCO	HUEL	Group 1	Group 2	Group 3
GATA053	N	112	59	24	16	24	24	25	15	2	2	116	113	15
	Allele													
	247	0	0	0	0	0.021	0	0	0	0	0	0.000	0.004	0.000
	257	0	0	0	0.063	0	0	0.02	0	0.25	0	0.003	0.013	0.000
	259	0	0	0	0	0.021	0	0	0	0	0	0.000	0.004	0.000
	261	0	0	0.063	0	0.042	0	0	0	0.25	0	0.003	0.022	0.000
	263	0	0	0	0	0.125	0.083	0	0.033	0	0	0.000	0.045	0.033
	265	0.728	0.729	0.792	0.938	0.771	0.917	0.86	0.933	0.5	1	0.729	0.848	0.933
	267	0	0	0	0	0	0	0	0.033	0	0	0.000	0.000	0.033
	269	0.272	0.271	0.146	0	0	0	0.12	0	0	0	0.266	0.058	0.000
	271	0	0	0	0	0.021	0	0	0	0	0	0.000	0.004	0.000

Appendix II. Haplotypes and variable sites for the mitochondrial control region (334pb) sequenced.

| mcr | Variable sites | | |

Appendix II. Continued.

| mcr | Variable sites | | |

Appendix II. Continued.

| mcr | Variable sites | | |

Appendix II. Continued.

| mcr | Variable sites | | |

Appendix II. Continued.

| mcr | Variable sites | | |

Appendix II. Continued.

mcr	Variable sites																						
Type	234	236	237	238	240	243	253	254	262	265	266	272	276	289	291	296	302	311	312	313	314	315	329
Hap_1	C	C	G	C	C	A	T	C	G	C	C	T	T	C	G	A	T	A	A	T	C	A	
Hap_2	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_5	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_7	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_17	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_19	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_21	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_22	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_23	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	

mcr	Variable sites																						
Type	234	236	237	238	240	243	253	254	262	265	266	272	276	289	291	296	302	311	312	313	314	315	329
Hap_24	.	T	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_26	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	
Hap_27	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	
Hap_29	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_31	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_32	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	
Hap_33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_34	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_35	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_36	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	
Hap_37	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_38	.	.	.	.	.	T	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_39	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	
hap_40	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	
Hap_41	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_42	.	.	A	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_43	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_44	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_45	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Hap_46	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	

Appendix II. Continued.

mcr	Variable sites																								
Type	234	236	237	238	240	243	253	254	262	265	266	272	276	289	291	296	302	312	313	314	315	329
Hap_47	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_48	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_49	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.
Hap_51	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_52	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_53	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_54	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_55	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_56	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_57	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_58	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_59	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_60	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_61	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_62	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_63	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_64	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_65	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_66	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_67	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_68	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

mcr	Variable sites																								
Type	234	236	237	238	240	243	253	254	262	265	266	272	276	289	291	296	302	312	313	314	315	329
Hap_69	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_70	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_71	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_72	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_73	.	.	A	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G
Hap_74	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_75	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_76	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_77	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.
Hap_78	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_79	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.
Hap_80	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_81	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_82	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_83	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_84	.	.	.	T	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_85	.	T	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_86	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_87	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.
Hap_88	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_89	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_90	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Appendix II. Continued.

mcr	Variable sites																					
Type	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3
	3	3	3	3	4	4	5	5	6	6	6	7	7	8	9	9	0	1	1	1	1	2
	4	6	7	8	0	3	3	4	2	5	6	2	6	9	1	6	2	2	3	4	5	9
Hap_69	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_70	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_71	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_72	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_73	.	.	A	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G
Hap_74	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_75	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_76	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_77	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.
Hap_78	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_79	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.
Hap_80	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_81	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_82	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_83	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_84	.	.	.	T	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_85	.	T	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_86	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_87	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.
Hap_88	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_89	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_90	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

mcr	Variable sites																					
Type	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3
	3	3	3	3	4	4	5	5	6	6	6	7	7	8	9	9	0	1	1	1	1	2
	4	6	7	8	0	3	3	4	2	5	6	2	6	9	1	6	2	2	3	4	5	9
Hap_91	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_92	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_93	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_94	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.
Hap_95	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_96	.	.	.	.	.	.	.	.	A	.	T	.	.	.	.	.	.	.	.	.	.	.
Hap_97	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_98	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_99	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.
Hap_100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_101	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_102	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_103	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.
Hap_104	T	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_105	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_106	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_107	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_108	.	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_109	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.
Hap_110	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hap_111	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Appendix III. Correspondence of haplotypes of this study and other previously published and accession numbers of GeneBank.

Haplotypes (in this study)	Haplotypes	Reference	GENEBANK Accession
Hap_1	FrM	Alfonsi et al 2012	HQ412587.1
	FrN	Alfonsi et al 2012	JF461060.1
	S6	Tolley & Rosel 2006	AY262375.1
	S9	Tolley & Rosel 2006	AY262378.1
	XXVIII	Viaud-Martínez et al 2007	EF063673.1
Hap_2	S13	Tolley & Rosel 2006	AY262382.1
	XXXI	Viaud-Martínez et al 2007	EF063676.1
Hap_3	D	Walton 1997	
	FrI	Alfonsi et al 2012	JF461058.1
	FrK	Alfonsi et al 2012	JF461059.1
	FrL	Alfonsi et al 2012	HQ412586.1
	GM90K18	Rosel et al 1999	AF311935.1
	N16	Tolley & Rosel 2006	GQ338869.1
	N4	Tolley et al 2001	AF311925.1
	N8	Tolley & Rosel 2006	GQ338862.1
	O	Walton 1997	
	S5	Tolley & Rosel 2006	AY262374.1
	S7	Tolley & Rosel 2006	AY262376.1
	S8	Tolley & Rosel 2006	AY262377.1
	V	Walton 1997	
	XXV	Viaud-Martínez et al 2007	EF063670.1
	XXVI	Viaud-Martínez et al 2007	EF063671.1
	XXVII	Viaud-Martínez et al 2007	EF063672.1
Hap_4	A	Walton 1997	X91613.1
	E	Walton 1997	
	FrB	Alfonsi et al 2012	JF461056.1
	FrC	Alfonsi et al 2012	HQ412580.1
	FrD	Alfonsi et al 2012	JF461057.1
	FrE	Alfonsi et al 2012	HQ412581.1
	FrO	Alfonsi et al 2012	JF461061.1
	N1	Tolley & Rosel 2006	AY262369.1
	N26	Tolley & Rosel 2006	GQ338874.1
	Pho1	Tiedemann et al 1996	Y13872.1
	Pho2	Tiedemann et al 1996	Y13875.1
	Pho24	Wiemann et al 2010	
	Pho42	Wiemann et al 2010	
	Pho7	Tiedemann et al 1996	Y13877.1
	S11	Tolley & Rosel 2006	AY262380.1
	XXIX	Viaud-Martínez et al 2007	EF063674.1
Hap_5			
Hap_6	S16	Tolley & Rosel 2006	AY262385.1

Appendix III. Continued.

Haplotypes (in this study)	Haplotypes	Reference	GENEBANK Accession
	XXX	Viaud-Martínez et al 2007	EF063675.1
Hap_7			
Hap_8			
Hap_9	C	Walton 1997	
	FrF	Alfonsi et al 2012	HQ412582.1
	GSL8921	Tolley et al 2001	FJ214755
	IC12 (GSL8902)	Rosel et al 1999	FJ214743.1
	L	Walton 1997	
	N11	Tolley & Rosel 2006	GQ338865.1
	N22	Tolley & Rosel 2006	GQ338872.1
	Pho19	Wiemann et al 2010	
	Pho4	Tiedemann et al 1996	Y13873.1
	Pho6	Tiedemann et al 1996	Y13880.1
	S1	Tolley & Rosel 2006	AY262370.1
	S12 (N12)	Tolley & Rosel 2006	AY262381.1
	S2	Tolley & Rosel 2006	AY262371.1
	XX	Viaud-Martínez et al 2007	EF063665.1
Hap_10	II	Viaud-Martínez et al 2007	EF063647.1
Hap_11	AH	Walton 1997	
	FrA	Alfonsi et al 2012	HQ412579.1
	N3	Tolley et al 2001	AF311924.1
	Pho45	Wiemann et al 2010	
	XIX	Viaud-Martínez et al 2007	EF063664.1
Hap_12	B	Walton 1997	
	IC3 (NFD800859)	Rosel et al 1999	FJ214766.1
	Pho3	Tiedemann et al 1996	Y13874.1
	Pho5	Tiedemann et al 1996	Y13876.1
	Pho8	Tiedemann et al 1996	Y13878.1
Hap_13	Pho9	Tiedemann et al 1996	Y13879.1
Hap_14	Pho10	Wiemann et al 2010	
	Pho11	Wiemann et al 2010	
Hap_15	Pho12	Wiemann et al 2010	
Hap_16	Pho13	Wiemann et al 2010	
Hap_17	Pho14	Wiemann et al 2010	
	S14 (N18)	Tolley & Rosel 2006	AY262383.1
Hap_18	Pho15	Wiemann et al 2010	
	Pho16	Wiemann et al 2010	
hap_19	Pho17	Wiemann et al 2010	
Hap_20	Pho18	Wiemann et al 2010	
Hap_21	H	Walton 1997	
	IC32 (GM90K13)	Rosel et al 1999	FJ214736.1
	N19	Tolley & Rosel 2006	GQ338871.1

Appendix III. Continued.

Haplotypes (in this study)	Haplotypes	Reference	GENEBANK Accession
	N20	Tolley et al 2001	AF311927.1
	Pho20	Wiemann et al 2010	
Hap_21	XXIV	Viaud-Martínez et al 2007	EF063669.1
Hap_22	FrJ	Alfonsi et al 2012	HQ412585.1
	N15	Tolley & Rosel 2006	GQ338868.1
	Pho23	Wiemann et al 2010	
Hap_23	IC26 (GSL8915)	Rosel et al 1999	FJ214751.1
	Pho25	Wiemann et al 2010	
Hap_24	Pho26	Wiemann et al 2010	
Hap_25	Pho27	Wiemann et al 2010	
Hap_26	Pho28	Wiemann et al 2010	
Hap_27	Pho29	Wiemann et al 2010	
Hap_28	Pho30	Wiemann et al 2010	
Hap_29	Pho32	Wiemann et al 2010	
Hap_30	Pho33	Wiemann et al 2010	
Hap_31	Pho34	Wiemann et al 2010	
	Pho36	Wiemann et al 2010	
Hap_32	Pho39	Wiemann et al 2010	
Hap_33	Pho40	Wiemann et al 2010	
	S3	Tolley & Rosel 2006	AY262372.1
Hap_34	Pho41	Wiemann et al 2010	
Hap_35	Pho46	Wiemann et al 2010	
Hap_36	Pho47	Wiemann et al 2010	
Hap_37	Pho48	Wiemann et al 2010	
Hap_38	Pho49	Wiemann et al 2010	
Hap_39	FrG	Alfonsi et al 2012	HQ412583.1
	S4	Tolley & Rosel 2006	AY262373.1
	XXII	Viaud-Martínez et al 2007	EF063667.1
Hap_40	FrH	Alfonsi et al 2012	HQ412584.1
	IC5	Tolley et al 2001	AF311932.1
Hap_41	AE	Walton 1997	
	AI	Walton 1997	
	S10	Tolley & Rosel 2006	AY262379.1
	XXI	Viaud-Martínez et al 2007	EF063666.1
Hap_42	XXIII	Viaud-Martínez et al 2007	EF063668.1
Hap_43	III	Viaud-Martínez et al 2007	EF063648.1
	XVI	Viaud-Martínez et al 2007	EF063661.1
Hap_44	I	Viaud-Martínez et al 2007	EF063646.1
	VIII	Viaud-Martínez et al 2007	EF063653.1
	XV	Viaud-Martínez et al 2007	EF063660.1
	XXXII	Viaud-Martínez et al 2007	EF063110.1
Hap_45	XVIII	Viaud-Martínez et al 2007	EF063663.1

Appendix III. Continued.

Haplotypes (in this study)	Haplotypes	Reference	GENEBANK Accession
Hap_46	XIV	Viaud-Martínez et al 2007	EF063659.1
Hap_47	XIII	Viaud-Martínez et al 2007	EF063658.1
Hap_48	XII	Viaud-Martínez et al 2007	EF063657.1
Hap_49	XI	Viaud-Martínez et al 2007	EF063656.1
Hap_50	X	Viaud-Martínez et al 2007	EF063655.1
Hap_51	IX	Viaud-Martínez et al 2007	EF063654.1
Hap_52	VII	Viaud-Martínez et al 2007	EF063652.1
Hap_53	VI	Viaud-Martínez et al 2007	EF063651.1
Hap_54	V	Viaud-Martínez et al 2007	EF063650.1
Hap_55	IV	Viaud-Martínez et al 2007	EF063649.1
Hap_56	XVII	Viaud-Martínez et al 2007	EF063662.1
Hap_57	IC16	Tolley et al 2001	GQ338849.1
Hap_57	K	Walton 1997	
Hap_58	M	Walton 1997	
Hap_59	P	Walton 1997	
Hap_60	R	Walton 1997	
Hap_61	W	Walton 1997	
Hap_62	X	Walton 1997	
Hap_63	Y		
Hap_64	AB	Walton 1997	
	IC7 (GSL8905)	Rosel et al 1999	FJ214745.1
	N29 (GSL8905)	Rosel et al 1999	FJ214745.1
Hap_65	AF	Walton 1997	
Hap_66	AG	Walton 1997	
Hap_67	AJ	Walton 1997	
Hap_68	AK	Walton 1997	
Hap_69	S15	Tolley & Rosel 2006	AY262384.1
Hap_70	S17	Tolley & Rosel 2006	AY262386.1
Hap_71	N2	Tolley & Rosel 2006	GQ338859.1
Hap_72	IC28	Tolley et al 2001	GQ338855.1
	N5	Rosel et al 1999	AF311926.1
Hap_73	N6	Tolley & Rosel 2006	GQ338860.1
Hap_74	N7	Tolley & Rosel 2006	GQ338861.1
Hap_75	N9	Tolley & Rosel 2006	GQ338863.1
Hap_76	IC10	Tolley et al 2001	GQ338846.1
Hap_76	N10	Tolley & Rosel 2006	GQ338864.1
Hap_77	N13	Tolley & Rosel 2006	GQ338866.1
Hap_78	N14	Tolley & Rosel 2006	GQ338867.1
Hap_79	N17	Tolley & Rosel 2006	GQ338870.1
Hap_80	N21	Tolley et al 2001	AF311928.1
Hap_81	N23	Tolley et al 2001	AF311929.1
Hap_82	N24	Tolley et al 2001	AF311930.1
Hap_83	N25	Tolley & Rosel 2006	GQ338873.1

Appendix III. Continued.

Haplotypes (in this study)	Haplotypes	Reference	GENEBANK Accession
Hap_84	N27	Tolley & Rosel 2006	GQ338875.1
Hap_85	IC14	Tolley et al 2001	AF311933.1
Hap_86	WGLD21	Rosel et al 1999	FJ214789.1
Hap_87	IC30	Tolley et al 2001	GQ338857.1
Hap_88	IC23	Tolley et al 2001	GQ338853.1
Hap_89	WGLD39	Rosel et al 1999	FJ214791.1
Hap_90	WGLD4	Rosel et al 1999	FJ214785.1
Hap_91	WGLD50	Rosel et al 1999	FJ214793.1
Hap_92	IC20	Tolley et al 2001	GQ338851.1
Hap_93	IC1	Tolley et al 2001	AF311931.1
Hap_94	IC29	Tolley et al 2001	GQ338856.1
Hap_95	9Pp28	Rosel et al 1999	FJ214781.1
Hap_96	GM90K02	Rosel et al 1999	AF311934.1
Hap_97	IC31	Tolley et al 2001	GQ338858.1
Hap_98	IC11	Tolley et al 2001	GQ338847.1
Hap_99	IC18	Tolley et al 2001	GQ338850.1
Hap_100	IC13	Tolley et al 2001	GQ338848.1
Hap_101	IC2	Tolley et al 2001	GQ338845.1
Hap_102	IC22	Tolley et al 2001	GQ338852.1
Hap_103	IC25 (WGLD47)	Rosel et al 1999	FJ214792.1
Hap_104	IC15 (GM90B41)	Rosel et al 1999	FJ214742.1
Hap_105	IC6 (GSL8935)	Rosel et al 1999	FJ214759.1
Hap_106	WGLD14	Rosel et al 1999	FJ214786.1
Hap_107	IC8 (WGLD34)	Rosel et al 1999	FJ214790.1
Hap_108	IC24 (GM90K05)	Rosel et al 1999	FJ214733.1
hap_109	IC17 (NFD910740)	Rosel et al 1999	FJ214774.1
Hap_110	WGLD17	Rosel et al 1999	FJ214788.1
Hap_111	WGLD15	Rosel et al 1999	FJ214787.1

Appendix IV. Occurrence of harbour porpoise mitochondrial haplotypes in the 9 populations geographical regions, and for K= 4.Population names as in Fig. 11.

mcr	Population										Population				
Type	SP	PT	NE1	NE2	WGLD	ICL	WA	AMS	BS	TOTAL	Group 1	Group 2	Group 3	Group 4	TOTAL
Hap_1	34	55	41							130	89	41			130
Hap_2	6	7	1							14	13	1			14
Hap_3	17	36	66			5	2			126	53	66	7		126
Hap_4	2		392	332		5	19			750	2	724	24		750
Hap_5		1								1	1				1
Hap_6	1	5					2			8	8				8
Hap_7		1								1	1				1
Hap_8		2								2	2				2
Hap_9			101	9		6	6			122		110	12		122
Hap_10			1						1	2	1			1	2
Hap_11			13							13		13			13
Hap_12			9	5		1	1			16		14	2		16
Hap_13			2	1						3		3			3
Hap_14				6						6		6			6
Hap_15				1						1		1			1
Hap_16				2						2		2			2
Hap_17		1	1	12						14	1	13			14
Hap_18				4						4		4			4
Hap_19				1						1		1			1
Hap_20				3						3		3			3
Hap_21			8	2		3	8			21	8	2	11		21
Hap_22			2	1						3		3			3
Hap_23				3			1			4		3	1		4
Hap_24			1							1		1			1
Hap_25				10						10		10			10
Hap_26			1							1		1			1
Hap_27			1							1		1			1
Hap_28				3						3		3			3
Hap_29			2	1						3		3			3
Hap_30			1							1		1			1
Hap_31			1	1						2		2			2
Hap_32			1							1		1			1
Hap_33			2							2		2			2
Hap_34			1							1		1			1
Hap_35				1						1		1			1
Hap_36				1						1		1			1
Hap_37				1						1		1			1
Hap_38				1						1		1			1
Hap_39			7							7		7			7

Appendix IV. Continued.

mcr Type	Population										Population				
	SP	PT	NE1	NE2	WGLD	ICL	WA	AMS	BS	TOTAL	Group 1	Group 2	Group 3	Group 4	TOTAL
hap_40			1			2				3		1	2		3
Hap_41			6							6		6			6
Hap_42			1							1		1			1
Hap_43									2	2				2	2
Hap_44								6	79	85				85	85
Hap_45								3		3				3	3
Hap_46									1	1				1	1
Hap_47									1	1				1	1
Hap_48									1	1				1	1
Hap_49									5	5				5	5
Hap_50									4	4				4	4
Hap_51									2	2				2	2
Hap_52									1	1				1	1
Hap_53									1	1				1	1
Hap_54									1	1				1	1
Hap_55									3	3				3	3
Hap_56									2	2				2	2
Hap_57			1			2				3		1	2		3
Hap_58			5							5		5			5
Hap_59			4							4		4			4
Hap_60			2							2		2			2
Hap_61			2							2		2			2
Hap_62			6							6		6			6
Hap_63			2							2		2			2
Hap_64			2			2				4		2	2		4
Hap_65			1							1		1			1
Hap_66			1							1		1			1
Hap_67			2							2		2			2
Hap_68			1							1		1			1
Hap_69							2			2	2				2
Hap_70							1			1	1				1
Hap_71			1			1				2		1	1		2
Hap_72			1		2	1				4		1	3		4
Hap_73			1							1		1			1
Hap_74			1							1		1			1
Hap_75			2							2		2			2
Hap_76			1			2				3		1	2		3
Hap_77			1							1		1			1
Hap_78			2							2		2			2
Hap_79			2			1				3		2	1		3

Appendix IV. Continued.

mcr Type	Population										Population				
	SP	PT	NE1	NE2	WGLD	ICL	WA	AMS	BS	TOTAL	Group 1	Group 2	Group 3	Group 4	TOTAL
Hap_80			1		4	3				8		1	7		8
Hap_81			1		3					4		1	3		4
Hap_82			1		2					3		1	2		3
Hap_83			1							1		1			1
Hap_84			1			1				2		1	1		2
Hap_85			1		2	1				4		1	3		4
Hap_86					1					1			1		1
Hap_87						3				3			3		3
Hap_88						1				1			1		1
Hap_89					1					1			1		1
Hap_90					1					1			1		1
Hap_91					1					1			1		1
Hap_92						1				1			1		1
Hap_93						2				2			2		2
Hap_94						1				1			1		1
Hap_95					3					3			3		3
Hap_96					2					2			2		2
Hap_97						1				1			1		1
Hap_98						1				1			1		1
Hap_99						1				1			1		1
Hap_100						1				1			1		1
Hap_101						1				1			1		1
Hap_102						1				1			1		1
Hap_103					1	1				2			2		2
Hap_104					2	1				3			3		3
Hap_105						1				1			1		1
Hap_106					1					1			1		1
Hap_107					1	1				2			2		2
Hap_108					1					1			1		1
Hap_109					1					1			1		1
Hap_110					1					1			1		1
Hap_111					1					1			1		1

Appendix V. Relative frequencies of harbour porpoise mitochondrial haplotypes for K= 4 and 9 populations. Population names as in Fig. 11.

mcr Type	Population								
	SP	PT	NE1	NE2	WGLD	ICL	WA	AMS	BS
N	60	108	715	401	47	75	5	4	104
Hap_1	0.567	0.509	0.057	0	0	0	0	0	0
Hap_2	0.1	0.065	0.001	0	0	0	0	0	0
Hap_3	0.283	0.333	0.092	0	0.106	0.027	0	0	0
Hap_4	0.033	0	0.548	0.828	0.106	0.253	0	0	0
Hap_5	0	0.009	0	0	0	0	0	0	0
Hap_6	0.017	0.046	0	0	0	0	0.400	0	0
Hap_7	0	0.009	0	0	0	0	0	0	0
Hap_8	0	0.019	0	0	0	0	0	0	0
Hap_9	0	0	0.141	0.022	0.128	0.080	0	0	0
Hap_10	0	0	0.001	0	0	0	0	0	0.010
Hap_11	0	0	0.018	0	0	0	0	0	0
Hap_12	0	0	0.013	0.012	0.0213	0.013	0	0	0
Hap_13	0	0	0.003	0.002	0	0	0	0	0
Hap_14	0	0	0	0.015	0	0	0	0	0
Hap_15	0	0	0	0.00249	0	0	0	0	0
Hap_16	0	0	0	0.005	0	0	0	0	0
Hap_17	0	0.009	0.001	0.030	0	0	0	0	0
Hap_18	0	0	0	0.010	0	0	0	0	0
Hap_19	0	0	0	0.003	0	0	0	0	0
Hap_20	0	0	0	0.007	0	0	0	0	0
Hap_21	0	0	0.011	0.005	0.064	0.107	0	0	0
Hap_22	0	0	0.003	0.003	0	0	0	0	0
Hap_28	0	0	0	0.007	0	0	0	0	0
Hap_29	0	0	0.003	0.002	0	0	0	0	0
Hap_30	0	0	0.001	0	0	0	0	0	0
Hap_31	0	0	0.001	0.002	0	0	0	0	0
Hap_32	0	0	0.001	0	0	0	0	0	0
Hap_33	0	0	0.003	0	0	0	0	0	0
Hap_34	0	0	0.001	0	0	0	0	0	0
Hap_35	0	0	0	0.002	0	0	0	0	0
Hap_36	0	0	0	0.002	0	0	0	0	0
Hap_37	0	0	0	0.002	0	0	0	0	0

mcr Type	Population			
	Group 1	Group 2	Group 3	Group 4
N	173	1107	123	108
Hap_1	0.514	0.037	0	0
Hap_2	0.075	0.001	0	0
Hap_3	0.306	0.060	0.057	0
Hap_4	0.012	0.654	0.195	0
Hap_5	0.006	0	0	0
Hap_6	0.046	0	0	0
Hap_7	0.006	0	0	0
Hap_8	0.012	0	0	0
Hap_9	0	0.091	0.098	0
Hap_10	0	0.001	0	0.009
Hap_11	0	0.012	0	0
Hap_12	0	0.013	0.016	0
Hap_13	0	0.003	0	0
Hap_14	0	0.005	0	0
Hap_15	0	0.001	0	0
Hap_16	0	0.002	0	0
Hap_17	0.006	0.012	0	0
Hap_18	0	0.004	0	0
Hap_19	0	0.001	0	0
Hap_20	0	0.003	0	0
Hap_21	0	0.009	0.089	0
Hap_22	0	0.003	0	0
Hap_28	0	0.003	0	0
Hap_29	0	0.003	0	0
Hap_30	0	0.001	0	0
Hap_31	0	0.002	0	0
Hap_32	0	0.001	0	0
Hap_33	0	0.002	0	0
Hap_34	0	0.001	0	0
Hap_35	0	0.001	0	0
Hap_36	0	0.001	0	0
Hap_37	0	0.001	0	0

Appendix V. Continued.

mcr	Population								
Type	SP	PT	NE1	NE2	WGLD	ICL	WA	AMS	BS
N	60	108	715	401	47	75	5	4	104
Hap_38	0	0	0	0.002	0	0	0	0	0
Hap_39	0	0	0.010	0	0	0	0	0	0
hap_40	0	0	0.001	0	0	0.027	0	0	0
Hap_41	0	0	0.008	0	0	0	0	0	0
Hap_42	0	0	0.001	0	0	0	0	0	0
Hap_43	0	0	0	0	0	0	0	0	0.019
Hap_44	0	0	0	0	0	0	0	0.250	0.760
Hap_45	0	0	0	0	0	0	0	0.750	0
Hap_46	0	0	0	0	0	0	0	0	0.010
Hap_47	0	0	0	0	0	0	0	0	0.010
Hap_48	0	0	0	0	0	0	0	0	0.010
Hap_49	0	0	0	0	0	0	0	0	0.050
Hap_50	0	0	0	0	0	0	0	0	0.040
Hap_51	0	0	0	0	0	0	0	0	0.019
Hap_52	0	0	0	0	0	0	0	0	0.010
Hap_53	0	0	0	0	0	0	0	0	0.010
Hap_54	0	0	0	0	0	0	0	0	0.010
Hap_55	0	0	0	0	0	0	0	0	0.030
Hap_56	0	0	0	0	0	0	0	0	0.019
Hap_57	0	0	0.001	0	0	0.027	0	0	0
Hap_58	0	0	0.007	0	0	0	0	0	0
Hap_59	0	0	0.006	0	0	0	0	0	0
Hap_60	0	0	0.003	0	0	0	0	0	0
Hap_61	0	0	0.0028	0	0	0	0	0	0
Hap_62	0	0	0.008	0	0	0	0	0	0
Hap_63	0	0	0.003	0	0	0	0	0	0
Hap_64	0	0	0.003	0	0	0.027	0	0	0
Hap_65	0	0	0.001	0	0	0	0	0	0
Hap_66	0	0	0.001	0	0	0	0	0	0
Hap_67	0	0	0.003	0	0	0	0	0	0
Hap_68	0	0	0.001	0	0	0	0	0	0
Hap_69	0	0	0	0	0	0	0.400	0	0

mcr	Population			
Type	Group 1	Group 2	Group 3	Group 4
N	173	1107	123	108
Hap_38	0	0.001	0	0
Hap_39	0	0.006	0	0
hap_40	0	0.001	0.016	0
Hap_41	0	0.005	0	0
Hap_42	0	0.001	0	0
Hap_43	0	0	0	0.018
Hap_44	0	0	0	0.009
Hap_45	0	0	0	0.028
Hap_46	0	0	0	0.009
Hap_47	0	0	0	0.009
Hap_48	0	0	0	0.009
Hap_49	0	0	0	0.046
Hap_50	0	0	0	0.037
Hap_51	0	0	0	0.018
Hap_52	0	0	0	0.009
Hap_53	0	0	0	0.009
Hap_54	0	0	0	0.009
Hap_55	0	0	0	0.028
Hap_56	0	0	0	0.018
Hap_57	0	0.001	0.016	0
Hap_58	0	0.004	0	0
Hap_59	0	0.004	0	0
Hap_60	0	0.002	0	0
Hap_61	0	0.002	0	0
Hap_62	0	0.005	0	0
Hap_63	0	0.002	0	0
Hap_64	0	0.002	0.016	0
Hap_65	0	0.001	0	0
Hap_66	0	0.001	0	0
Hap_67	0	0.002	0	0
Hap_68	0	0.001	0	0
Hap_69	0.012	0	0	0

Appendix V. Continued.

mcr Type	Population								
	SP	PT	NE1	NE2	WGLD	ICL	WA	AMS	BS
N	60	108	715	401	47	75	5	4	104
Hap_70	0	0	0	0	0	0	0.200	0	0
Hap_71	0	0	0.001	0	0	0.013	0	0	0
Hap_72	0	0	0.001	0	0.043	0.013	0	0	0
Hap_73	0	0	0.001	0	0	0	0	0	0
Hap_74	0	0	0.001	0	0	0	0	0	0
Hap_75	0	0	0.003	0	0	0	0	0	0
Hap_76	0	0	0.001	0	0	0.027	0	0	0
Hap_77	0	0	0.001	0	0	0	0	0	0
Hap_78	0	0	0.003	0	0	0	0	0	0
Hap_79	0	0	0.003	0	0	0.013	0	0	0
Hap_80	0	0	0.001	0	0.085	0.040	0	0	0
Hap_81	0	0	0.001	0	0.064	0	0	0	0
Hap_82	0	0	0.001	0	0.043	0	0	0	0
Hap_83	0	0	0.001	0	0	0	0	0	0
Hap_84	0	0	0.001	0	0	0.013	0	0	0
Hap_85	0	0	0.001	0	0.043	0.013	0	0	0
Hap_86	0	0	0	0	0.021	0	0	0	0
Hap_87	0	0	0	0	0	0.040	0	0	0
Hap_88	0	0	0	0	0	0.013	0	0	0
Hap_89	0	0	0	0	0.021	0	0	0	0
Hap_90	0	0	0	0	0.021	0	0	0	0
Hap_91	0	0	0	0	0.021	0	0	0	0
Hap_92	0	0	0	0	0	0.013	0	0	0
Hap_93	0	0	0	0	0	0.027	0	0	0
Hap_94	0	0	0	0	0	0.013	0	0	0
Hap_95	0	0	0	0	0.064	0	0	0	0
Hap_96	0	0	0	0	0.043	0	0	0	0
Hap_97	0	0	0	0	0	0.013	0	0	0
Hap_98	0	0	0	0	0	0.013	0	0	0
Hap_99	0	0	0	0	0	0.013	0	0	0
Hap_100	0	0	0	0	0	0.013	0	0	0

mcr Type	Population			
	Group 1	Group 2	Group 3	Group 4
N	173	1107	123	108
Hap_70	0.006	0	0	0
Hap_71	0	0.001	0.008	0
Hap_72	0	0.001	0.024	0
Hap_73	0	0.001	0	0
Hap_74	0	0.001	0	0
Hap_75	0	0.002	0	0
Hap_76	0	0.001	0.016	0
Hap_77	0	0.001	0	0
Hap_78	0	0.002	0	0
Hap_79	0	0.002	0.008	0
Hap_80	0	0.001	0.0569	0
Hap_81	0	0.001	0.024	0
Hap_82	0	0.001	0.016	0
Hap_83	0	0.001	0	0
Hap_84	0	0.001	0.008	0
Hap_85	0	0.001	0.016	0
Hap_86	0	0	0.024	0
Hap_87	0	0	0.024	0
Hap_88	0	0	0.008	0
Hap_89	0	0	0.008	0
Hap_90	0	0	0.008	0
Hap_91	0	0	0.008	0
Hap_92	0	0	0.008	0
Hap_93	0	0	0.016	0
Hap_94	0	0	0.008	0
Hap_95	0	0	0.0244	0
Hap_96	0	0	0.016	0
Hap_97	0	0	0.008	0
Hap_98	0	0	0.008	0
Hap_99	0	0	0.008	0
Hap_100	0	0	0.008	0

Appendix V. Continued.

mcr Type	Population								
	SP	PT	NE1	NE2	WGLD	ICL	WA	AMS	BS
N	60	108	715	401	47	75	5	4	104
Hap_101	0	0	0	0	0	0.013	0	0	0
Hap_102	0	0	0	0	0	0.013	0	0	0
Hap_103	0	0	0	0	0.021	0.013	0	0	0
Hap_104	0	0	0	0	0.043	0.013	0	0	0
Hap_105	0	0	0	0	0	0.013	0	0	0
Hap_106	0	0	0	0	0.021	0	0	0	0
Hap_107	0	0	0	0	0.021	0.013	0	0	0
Hap_108	0	0	0	0	0	0.013	0	0	0
Hap_109	0	0	0	0	0	0.013	0	0	0
Hap_110	0	0	0	0	0	0.013	0	0	0
Hap_111	0	0	0	0	0	0.013	0	0	0

mcr Type	Population			
	Group 1	Group 2	Group 3	Group 4
N	173	1107	123	108
Hap_101	0	0	0.008	0
Hap_102	0	0	0.008	0
Hap_103	0	0	0.016	0
Hap_104	0	0	0.0244	0
Hap_105	0	0	0.008	0
Hap_106	0	0	0.008	0
Hap_107	0	0	0.016	0
Hap_108	0	0	0.008	0
Hap_109	0	0	0.008	0
Hap_110	0	0	0.008	0
Hap_111	0	0	0.008	0

Appendix VI. Models for the study of the covariates affecting the observer. P-values: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. Covariates: width of field (width_field), speed, Douglas, Beaufort, Easting component of the wind (Wind Easting, Sen_WRad_), Northing component of the wind (Wind Northing, Cos_WRad_), visibility, height of the swell (Swell height), ship.

Model	Covariate									Dev. Expl.	AIC
	width field	Speed	Douglas	Beaufort	Wind Easting	Wind Northing	Visibility	Swell height	Ship		
Y~ 1 + s(Douglas. k = 3) + s(Speed) + s(Sen_WRad_. k = 3)		.97e-06 ***	1.32e-15 ***		0.314					14.20%	257.06
Y~ 1 + s(Douglas. k = 3) + s(Speed) + s(Cos_WRad_. k = 3)		4.39e-06 ***	1.25e-15 ***			0.493				14.20%	257.12
Y ~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3) + s(Sen_WRad_. k = 3)	1.94e-05 ***	9.56e-06 ***	9.32e-12 ***		0.273					14.80%	257.26
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3) + s(Cos_WRad_. k = 3)	3.20e-05 ***	8.58e-06 ***	1.50e-11 ***			0.935				14.70%	257.42
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3) + s(Visib. k = 3) + s(Sen_WRad_. k = 3)	2.17e-07 ***	5.09e-06 ***	1.54e-10 ***		0.10951		0.00105 **			15.30%	257.91
Y ~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3) + s(Visib. k = 3) + s(Cos_WRad_. k = 3)	8.43e-07 ***	4.71e-06 ***	1.70e-10 ***			0.80441	0.00219 **			15.20%	258.22
Y~ 1 + as.factor(Ship) + s(Douglas. k = 3) + s(Speed) + s(Cos_WRad_. k = 3)		3.05e-05 ***	9.27e-15 ***			0.38			0.0104 *	14.40%	258.26
Y ~ 1 + as.factor(Ship) + s(Douglas. k = 3) + s(Speed) + s(Sen_WRad_. k = 3)		3.18e-05 ***	1.03e-14 ***		0.397				0.0137 *	14.40%	258.27
Y~ 1 + s(Douglas. k = 3) + s(Speed) + s(Beaufort. k = 3) + s(Sen_WRad_. k = 3)		1.64e-05 ***	8.38e-11 ***	0.0669	0.2833					14.30%	258.72
Y~ 1 + s(Douglas. k = 3) + s(Speed) + s(Beaufort. k = 3) + s(Cos_WRad_. k = 3)		1.45e-05 ***	7.94e-11 ***	0.0701 .		0.4743				14.30%	258.79
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3) + s(Beaufort. k = 3) + s(Sen_WRad_. k = 3)	0.000124 ***	9.26e-06 ***	1.42e-09 ***	0.404126	0.267772					14.80%	259.21
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3) + s(Beaufort. k = 3) + s(Cos_WRad_. k = 3)	7.91e-05 ***	1.08e-05 ***	< 2e-16 ***	0.232		0.837				14.10%	260.06
Y~ 1 + s(Beaufort. k = 3) + s(Speed) + s(Visib. k = 3) + s(Sen_WRad_. k = 3) + s(Douglas. k = 3)		3.42e-06 ***	1.31e-10 ***	0.0763 .	0.1854		0.0790 .			14.50%	260.26

Appendix VI. Continued.

Model	Covariate									Dev. Expl.	AIC
	width field	Speed	Douglas	Beaufort	Wind Easting	Wind Northing	Visibility	Swell height	Ship		
Y~ 1 + s(Width_Field. k = 3) + s(Douglas. k = 3) + s(Sen_WRad_. k = 3)	2.87e-07 ***		< 2e-16 ***		0.34					11.50%	260.92
Y~ 1 + s(Width_Field. k = 3) + s(Douglas. k = 3) + s(Cos_WRad_. k = 3)	3.36e-07 ***		< 2e-16 ***			0.488				11.50%	260.98
Y~ 1 + as.factor(Ship) + s(Douglas. k = 3) + s(Sen_WRad_. k = 3)			<2e-16 ***		0.551				0.000142 ***	11.30%	261.45
Y ~ 1 + as.factor(Ship) + s(Douglas. k = 3) + s(Cos_WRad_. k = 3)			<2e-16 ***			0.553			0.000115 ***	11.30%	261.45
Y~ 1 + s(Douglas. k = 3) + s(Sen_WRad_. k = 3)			<2e-16 ***		0.471					10.50	261.86
Y~ 1 + s(Douglas. k = 3) + s(Cos_WRad_. k = 3)			<2e-16 ***			0.911				10.50%	261.92
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Visib. k = 3) + s(Sen_WRad_. k = 3)	< 2e-16 ***	1.28e-06 ***			0.0504		2.66e-11 ***			11.50%	267.04
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Visib. k = 3) + s(Cos_WRad_. k = 3)	< 2e-16 ***	1.49e-06 ***				0.665	3.63e-10 ***			11.30%	267.51
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Beaufort. k = 3) + s(Sen_WRad_. k = 3)	1.47e-09 ***	7.63e-06 ***		1.52e-09 ***	0.236					10.50%	268.36
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Beaufort. k = 3) + s(Cos_WRad_. k = 3)	1.47e-09 ***	7.31e-06 ***		3.74e-09 ***		0.524				10.40%	268.47
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Cos_WRad_. k = 3)	< 2e-16 ***	1.05e-05 ***				0.183				9.59%	270.24
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Sen_WRad_. k = 3)	< 2e-16 ***	1.03e-05 ***			0.302					9.58%	270.31
Y ~ 1 + s(Beaufort. k = 3) + s(Speed) + s(Sen_WRad_. k = 3)		3.89e-06 ***		< 2e-16 ***	0.159					9.13%	270.31
Y~ 1 + s(Beaufort. k = 3) + s(Speed) + s(Cos_WRad_. k = 3)		3.17e-06 ***		< 2e-16 ***		0.525				9.07%	270.47
Y~ 1 + s(Beaufort. k = 3) + s(Speed) + s(Visib. k = 3) + s(Sen_WRad_. k = 3)		2.14e-06 ***		< 2e-16 ***	0.06716 .		0.00138 **			9.61%	270.97
Y~ 1 + s(Beaufort. k = 3) + s(Speed) + s(Visib. k = 3) + s(Cos_WRad_. k = 3)		1.82e-06 ***		< 2e-16 ***		0.28562	0.00197 **			9.53%	271.2

Appendix VI. Continued.

Model	Covariate									Dev. Expl.	AIC
	width field	Speed	Douglas	Beaufort	Wind Easting	Wind Northing	Visibility	Swell height	Ship		
Y~ 1 + as.factor(Ship) + s(Beaufort. k = 3) + s(Speed) + s(Sen_WRad_. k = 3)		2.16e-05 ***		4.97e-16 ***	0.191				0.105	9.18%	271.99
Y ~ 1 + as.factor(Ship) + s(Beaufort. k = 3) + s(Speed) + s(Cos_WRad_. k = 3)		1.99e-05 ***		5.43e-16 ***		0.413			0.078 .	9.15%	272.1
Y~ 1 + as.factor(Ship) + s(Beaufort. k = 3) + s(Speed) + s(Visib. k = 3) + s(Sen_WRad_. k = 3)		1.09e-05 ***		6.82e-15 ***	0.07802 .		0.00161 **		0.121	9.66%	272.69
Y ~ 1 + as.factor(Ship) + s(Beaufort. k = 3) + s(Speed) + s(Visib. k = 3) + s(Cos_WRad_. k = 3)		1.16e-05 ***		8.56e-15 ***		0.20589	0.00208 **		0.082 .	9.60%	272.84
Y~ 1 + s(Beaufort. k = 3) + s(Speed) + s(Visib. k = 3) + s(Sen_WRad_. k = 3) + s(Cos_WRad_. k = 3)		8.9e-07 ***		< 2e-16 ***	0.1065	0.51375	0.00114 **			9.64%	272.9
Y~ 1 + as.factor(Ship) + s(Beaufort. k = 3) + s(Sen_WRad_. k = 3)				1.13e-15 ***	0.204				7.22e-05 ***	6.59%	274.97
Y~ 1 + as.factor(Ship) + s(Beaufort. k = 3) + s(Cos_WRad_. k = 3)				1.27e-15 ***		0.576			4.42e-05 ***	6.53%	275.14
Y ~ 1 + s(Width_Field. k = 3) + s(Cos_WRad_. k = 3)	<2e-16 ***					0.0136 *				5.65%	275.65
Y~ 1 + s(Beaufort. k = 3) + s(Sen_WRad_. k = 3)				<2e-16 ***	0.107					5.60%	275.8
Y~ 1 + s(Beaufort. k = 3) + s(Cos_WRad_. k = 3)				<2e-16 ***	0.864					5.48%	276.14
Y ~ 1 + s(Width_Field. k = 3) + s(Sen_WRad_. k = 3)	<2e-16 ***				0.248					5.44%	276.27
Y ~ 1 + s(Beaufort. k = 3) + s(Visib. k = 3) + s(Sen_WRad_. k = 3)				<2e-16 ***	0.0627 .		0.0104 *			5.89%	276.97
Y~ 1 + s(Beaufort. k = 3) + s(Visib. k = 3) + s(Cos_WRad_. k = 3)				<2e-16 ***		0.8531	0.0177 *			5.73%	277.43
Y ~ 1 + s(Douglas. k = 3) + s(Speed)		9.56e-06 ***	4.46e-15 ***							12.90%	278.44
Y~ 1 + s(Douglas. k = 3) + s(Speed) + s(Beaufort. k = 3)		4.93e-06 ***	1.79e-11 ***	0.00194 **						13.90%	278.55
Y ~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3)	0.000178 ***	1.77e-05 ***	5.44e-12 ***							13.30%	279.07
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3) + s(Beaufort. k = 3)	0.000115 ***	9.13e-06 ***	4.61e-10 ***	0.002314 **						14.30%	279.15
Y~ 1 + as.factor(Ship) + s(Douglas. k = 3) + s(Speed)		2.84e-05 ***	2.76e-14 ***						0.0084 **	13.20%	279.47

Appendix VI. Continued.

Model	Covariate									Dev. Expl.	AIC
	width field	Speed	Douglas	Beaufort	Wind Easting	Wind Northing	Visibility	Swell height	Ship		
Y ~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3) + s(Visib. k = 3)	6.79e-06 ***	1.40e-05 ***	5.86e-11 ***				0.00858 **			13.60%	280.18
Y~ 1 + s(Douglas. k = 3) + s(Speed) + s(Visib. k = 3)		3.26e-06 ***	1.55e-14 ***				0.23			13.00%	280.19
Y~ 1 + s(Douglas. k = 3) + s(Speed) + s(Beaufort. k = 3) + s(Visib. k = 3)		4.32e-06 ***	2.38e-11 ***	0.00227 **			0.31764			13.90%	280.36
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3) + s(Visib. k = 3) + s(Beaufort. k = 3)	5.16e-06 ***	2.69e-06 ***	1.14e-09 ***	0.00338 **			0.01323 *			14.60%	280.37
Y~ 1 + as.factor(Ship) + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3)	0.00146 **	7.08e-05 ***	8.38e-12 ***						0.0386 *	13.50%	280.48
Y ~ 1 + as.factor(Ship) + s(Speed) + s(Visib. k = 3) + s(Sen_WRad_. k = 3)		1.05e-05 ***			0.183		8.81e-06 ***		0.000148 ***	6.23%	280.5
Y ~ 1 + as.factor(Ship) + s(Speed) + s(Visib. k = 3) + s(Cos_WRad_. k = 3)		1.09e-05 ***				0.327	1.03e-05 ***		0.000102 ***	6.21%	280.58
Y~ 1 + s(Speed) + s(Visib. k = 3) + s(Sen_WRad_. k = 3)		6.42e-07 ***			0.123		1.33e-06 ***			5.52%	280.81
Y~ 1 + s(Speed) + s(Visib. k = 3) + s(Cos_WRad_. k = 3)		5.28e-07 ***				0.48	2.40e-06 ***			5.45%	281.03
Y~ 1 + as.factor(Ship) + s(Beaufort. k = 3) + s(Speed) + s(Douglas. k = 3)		4.94e-05 ***	6.17e-14 ***	0.12					0.00316 **	13.20%	281.16
Y~ 1 + as.factor(Ship) + s(Douglas. k = 3) + s(Speed) + s(Visib. k = 3)		5.07e-05 ***	7.14e-14 ***				0.329		0.0102 *	13.20%	281.29
Y~ 1 + s(Speed) + s(Sen_WRad_. k = 3)		2.9e-06 ***			0.33					4.47%	281.73
Y~ 1 + s(Speed) + s(Cos_WRad_. k = 3)		5.28e-07 ***				0.887				4.43%	281.84
Y~ 1 + as.factor(Ship) + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3) + (Beaufort. k = 3)	0.000401 ***	3.40e-05 ***	1.84e-12 ***	0.032423 *					0.0104 *	13.60%	281.92
Y~ 1 + as.factor(Ship) + s(Beaufort. k = 3) + s(Speed) + s(Visib. k = 3) + s(Douglas. k = 3)		5.41e-05 ***	9.33e-14 ***	0.122			0.337		0.00387 **	13.30%	282.99

Appendix VI. Continued.

Model	Covariate									Dev. Expl.	AIC
	width field	Speed	Douglas	Beaufort	Wind Easting	Wind Northing	Visibility	Swell height	Ship		
Y ~ 1 + as.factor(Ship) + s(Douglas. k = 3)			<2e-16 ***						2.30e-05 ***	8.80%	286.84
Y~ 1 + as.factor(Ship) + s(Width_Field. k = 3) + s(Douglas. k = 3)	4.53e-05 ***		< 2e-16 ***						0.000242 ***	9.44%	286.87
Y ~ 1 + s(Width_Field. k = 3) + s(Douglas. k = 3)	7.04e-07 ***		< 2e-16 ***							8.72%	287.10
Y ~ 1 + s(Douglas. k = 3)			<2e-16 ***							7.780%	287.98
Y~ 1 + as.factor(Ship) + s(Douglas. k = 3) + s(Beaufort. k = 3)			<2e-16 ***	0.0579 .					7.18e-06 ***	8.95%	288.38
Y~ 1 + s(Width_Field. k = 3) + s(Douglas. k = 3) + s(Beaufort. k = 3)	1.53e-07 ***		< 2e-16 ***	0.0719						8.85%	288.69
Y~ 1 + s(Width_Field. k = 3) + s(Douglas. k = 3) + s(Visib. k = 3)	9.66e-08 ***		< 2e-16 ***				0.0919			8.83%	288.74
Y~ 1 + as.factor(Ship) + s(Douglas. k = 3) + s(Visib. k = 3)			<2e-16 ***				0.684		2.30e-05 ***	8.81%	288.82
Y ~ 1 + s(Sen_WRad_. k = 3)					0.209					0.079%	289.58
Y ~ 1 + s(Cos_WRad_. k = 3)						0.206				0.079%	289.58
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Visib. k = 3)	< 2e-16 ***	7.53e-06 ***					1.37e-09 ***			9.81%	289.75
Y ~ 1 + s(Douglas. k = 3) + s(Beaufort. k = 3)			<2e-16 ***	0.46						7.81%	289.91
Y~ 1 + s(Beaufort. k = 3) + s(Douglas. k = 3)			<2e-16 ***	0.46						7.81%	289.91
Y~ 1 + s(Douglas. k = 3) + s(Visib. k = 3)			<2e-16 ***				0.697			7.79%	289.96
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Beaufort. k = 3) + s(Visib. k = 3)	3.84e-10 ***	1.93e-07 ***		0.00393 **			1.45e-06 ***			9.94%	290.93
Y~ 1 + as.factor(Ship) + s(Width_Field. k = 3) + s(Speed) + s(Visib. k = 3)	2.48e-15 ***	1.60e-06 ***					7.00e-09 ***		0.13	9.82%	291.51
Y~ 1 + s(Width_Field. k = 3) + s(Speed) + s(Beaufort. k = 3)	1.69e-10 ***	1.87e-05 ***		3.13e-06 ***						8.76%	291.63
Y~ 1 + s(Beaufort. k = 3) + s(Visib. k = 3) + s(Douglas. k = 3)			<2e-16 ***	0.462			0.702			7.81%	291.89

Appendix VI. Continued.

Model	Covariate									Dev. Expl.	AIC
	width field	Speed	Douglas	Beaufort	Wind Easting	Wind Northing	Visibility	Swell height	Ship		
Y ~ 1 + s(Width_Field. k = 3) + s(Speed)	6.30e-15 ***	2.49e-07 ***								8.34%	292.04
Y~ 1 + as.factor(Ship) + s(Width_Field. k = 3) + s(Speed) + s(Douglas. k = 3) + s(Visib. k = 3)	9.67e-05 ***	5.23e-05 ***	7.24e-11 ***	2.22e-05 ***			0.0195 *		0.0748	8.83%	293.29
Y~ 1 + as.factor(Ship) + s(Width_Field. k = 3) + s(Speed) + s(Beaufort. k = 3)	2.10e-09 ***	7.19e-05 ***							0.106	8.83%	293.29
Y~ 1 + as.factor(Ship) + s(Width_Field. k = 3) + s(Speed)	3.68e-12 ***	8.37e-05 ***							0.0309 *	8.38%	293.51
Y~ 1 + s(Beaufort. k = 3) + s(Speed)		8.55e-06 ***		4.88e-14 ***						7.33%	294.08
Y~ 1 + as.factor(Ship) + s(Beaufort. k = 3) + s(Speed)		6.34e-05 ***		1.63e-11 ***					0.0153 *	7.55%	295.23
Y~ 1 + s(Beaufort. k = 3) + s(Speed) + s(Visib. k = 3)		6.79e-06 ***		1.45e-12 ***			0.0188 *			7.57%	295.35
Y ~ 1 + as.factor(Ship) + s(Beaufort. k = 3) + s(Speed) + s(Visib. k = 3)		5.00e-06 ***		2.61e-10 ***			0.0283 *		0.0203 *	7.77%	296.58
Y~ 1 + as.factor(Ship) + s(Width_Field. k = 3)	<2e-16 ***								7.36e-06 ***	5.44%	297.2
Y ~ 1 + s(Width_Field. k = 3) + s(Visib. k = 3)	< 2e-16 ***						1.7e-07 ***			5.27%	297.71
Y~ 1 + s(Swell height. k = 3)								0.593		0.05%	297.95
Y~ 1 + s(Width_Field. k = 3) + s(Beaufort. k = 3)	1.36e-12 ***			6.60e-06 ***						5.17%	298.02
Y ~ 1 + s(Width_Field. k = 3)	<2e-16 ***									4.24%	298.89
Y~ 1 + as.factor(Ship) + s(Beaufort. k = 3)				7.92e-11 ***					3.57e-06 ***	4.62%	299.71
Y~ 1 + as.factor(Ship) + s(Speed)		2.19e-05 ***							4.73e-05 ***	5.41%	299.81
Y~ 1 + as.factor(Ship) + s(Speed) + s(Visib. k = 3)		2.86e-05 ***					0.000398 ***		0.000118 ***	5.93%	300.23
Y ~ 1 + s(Speed)		2.81e-06 ***								4.57%	300.66
Y~ 1 + s(Speed) + s(Visib. k = 3)		1.37e-06 ***					6.34e-05 ***			5.21%	300.69

Appendix VI. Continued.

Model	Covariate									Dev. Expl.	AIC
	width field	Speed	Douglas	Beaufort	Wind Easting	Wind Northing	Visibility	Swell height	Ship		
Y~ 1 + as.factor(Ship) + s(Beaufort. k = 3) + s(Visib. k = 3)				5.75e-10 ***			0.0905 .		3.95e-06 ***	4.74%	301.35
Y ~ 1 + s(Beaufort. k = 3)				1.41e-15 ***						3.29%	301.82
Y~ 1 + s(Beaufort. k = 3) + s(Visib. k = 3)				1.55e-14 ***			0.0713 .			3.43%	303.4
Y ~ 1 + as.factor(Ship)									1.83e-09 ***	2.59%	303.99
Y ~ 1 + s(Visib. k = 3)							0.00132 **			0.4220%	310.65

Appendix VII. Models for the study of the environmental covariate with their values of Deviation Explained (Dev. Expl.) and AIC. Variables abbreviations: sea surface temperature (SST), chlorophyll concentration (CHL), euphotic depth (ZEU), photosynthetically active radiation (PAR), depth (DEP), seabed slope (DEP_SL), seabed aspect (DEP-AS), and their standard deviations (SST-STD, CHL-STD, ZEU-STD, PAR-STD, DEP-STD, DEP_SL-STD, DEP-AS-STD).

Model ID	Model	Dev. Expl.	AIC
MOD_001	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4)	26.50%	259.39
MOD_002	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4)	26.00%	259.60
MOD_003	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3)	26.00%	259.90
MOD_004	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4)	26.00%	260.16
MOD_005	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4)	26.00%	260.50
MOD_006	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4)	25.90%	260.52
MOD_007	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4)	25.90%	260.54
MOD_008	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4)	25.90%	260.55
MOD_009	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Depth, k = 4)	25.90%	260.60
MOD_010	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(Year, k = 4)	25.90%	260.70
MOD_011	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4)	25.90%	260.74
MOD_012	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Depth, k = 4)	25.80%	260.77
MOD_013	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3)	25.80%	260.78
MOD_014	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4)	25.70%	260.83
MOD_015	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Year, k = 4)	25.70%	261.01
MOD_016	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(Depth, k = 4)	25.70%	261.30
MOD_017	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(DEP, k = 4)	25.70%	261.32
MOD_018	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(DEP, k = 4)	25.70%	261.34
MOD_019	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(PAR_STD, k = 4)	25.70%	261.36
MOD_020	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(PAR_STD, k = 4)	25.60%	261.47
MOD_021	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Year, k = 4)	25.60%	261.47
MOD_022	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(PAR, k = 4)	25.60%	261.48

Model ID	Model	Dev. Expl.	AIC
MOD_023	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4)	25.60%	261.60
MOD_024	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4)	25.60%	261.61
MOD_025	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4)	25.60%	261.64
MOD_026	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(DEP, k = 4)	25.60%	261.66
MOD_027	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4)	25.50%	261.70
MOD_028	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Year, k = 4) + s(Depth, k = 4)	25.50%	261.70
MOD_029	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4)	25.50%	261.71
MOD_030	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Year, k = 4)	25.50%	261.75
MOD_031	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(Depth, k = 4)	25.50%	261.75
MOD_032	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(DEP_AS_Sin, k = 3)	25.50%	261.79
MOD_033	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Depth, k = 4)	25.50%	261.79
MOD_034	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4)	25.30%	261.85
MOD_035	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR_STD, k = 4)	25.30%	261.88
MOD_036	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Depth, k = 4)	25.30%	261.89
MOD_037	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3)	25.30%	261.90
MOD_038	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(Depth, k = 4)	25.30%	261.92
MOD_039	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(PAR, k = 4) + s(DEP_AS_Cos, k = 3)	25.30%	262.01
MOD_040	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(Year, k = 4)	25.30%	262.02
MOD_041	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(DEP, k = 4)	25.20%	262.02
MOD_042	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Depth, k = 4)	25.20%	262.03
MOD_043	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(PAR_STD, k = 4)	25.20%	262.13
MOD_044	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Depth, k = 4) + s(DEP_AS_Cos, k = 3)	25.20%	262.20
MOD_045	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(DEP_AS_Sin, k = 3)	25.20%	262.27
MOD_046	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(DEP_AS_Sin, k = 3)	25.20%	262.29

Model ID	Model	Dev. Expl.	AIC
MOD_047	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(Year, k = 4)	25.10%	262.31
MOD_048	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Year, k = 4) + s(Depth, k = 4) + s(Month, k = 4)	25.10%	262.31
MOD_049	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(DEP, k = 4)	25.10%	262.45
MOD_050	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(DEP, k = 4)	25.10%	262.48
MOD_051	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	25.10%	262.48
MOD_052	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(PAR_STD, k = 4)	25.10%	262.48
MOD_053	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(PAR_STD, k = 4)	25.10%	262.50
MOD_054	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(DEP, k = 4)	25.00%	262.50
MOD_055	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(DEP, k = 4)	25.00%	262.51
MOD_056	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(PAR_STD, k = 4)	25.00%	262.54
MOD_057	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(DEP_AS_Sin, k = 3)	25.00%	262.55
MOD_058	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(PAR, k = 4) + s(Depth, k = 4)	25.00%	262.56
MOD_059	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 3)	25.00%	262.58
MOD_060	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	25.00%	262.59
MOD_061	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(DEP, k = 4)	25.00%	262.61
MOD_062	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Year, k = 4) + s(Depth, k = 4)	25.00%	262.61
MOD_063	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(PAR_STD, k = 4)	25.00%	262.62
MOD_064	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(ZEU_STD, k = 4)	24.90%	262.63
MOD_065	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(Year, k = 4)	24.90%	262.65
MOD_066	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(PAR_STD, k = 4)	24.90%	262.65
MOD_067	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Depth, k = 4) + s(DEP_AS_Cos, k = 3)	24.90%	262.66
MOD_068	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(DEP_AS_Sin, k = 3)	24.80%	262.67

Model ID	Model	Dev. Expl.	AIC
MOD_069	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Year, k = 4) + s(DEP, k = 4)	24.80%	262.71
MOD_070	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(DEP, k = 4)	24.80%	262.73
MOD_071	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(PAR_STD, k = 4)	24.80%	262.79
MOD_072	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4)	24.80%	262.79
MOD_073	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4)	24.80%	262.82
MOD_074	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4)	24.80%	262.84
MOD_075	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(DEP, k = 4)	24.70%	262.84
MOD_076	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Year, k = 4) + s(DEP_AS_Sin, k = 3)	24.70%	262.90
MOD_077	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Depth, k = 4)	24.70%	262.95
MOD_078	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Year, k = 4) + s(PAR_STD, k = 4)	24.70%	262.98
MOD_079	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4)	24.70%	263.00
MOD_080	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Year, k = 4) + s(Depth, k = 4) + s(PAR, k = 4)	24.70%	263.03
MOD_081	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(PAR_STD, k = 4)	24.60%	263.03
MOD_082	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(ZEU_STD, k = 4)	24.60%	263.11
MOD_083	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Depth, k = 4)	24.60%	263.14
MOD_084	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Depth, k = 4) + s(ZEU_STD, k = 4)	24.50%	263.15
MOD_085	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(PAR, k = 4) + s(Year, k = 4)	24.50%	263.18
MOD_086	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(PAR, k = 4) + s(DEP, k = 4)	24.50%	263.22
MOD_087	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST,k = 4)	24.50%	263.31
MOD_088	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(SST, k = 4) + s(ZEU, k = 4)	24.50%	263.31
MOD_089	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(PAR, k = 4) + s(PAR_STD, k = 4)	24.50%	263.33
MOD_090	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(DEP_AS_Sin, k = 3)	24.50%	263.34
MOD_091	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(DEP_AS_Cos, k = 3)	24.40%	263.34
MOD_092	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(PAR, k = 4)	24.40%	263.35
MOD_093	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(Depth, k = 4)	24.40%	263.42

Model ID	Model	Dev. Expl.	AIC
MOD_094	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	24.40%	263.44
MOD_095	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(DEP_AS_Sin, k = 3)	24.40%	263.45
MOD_096	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Year, k = 4) + s(DEP, k = 4)	24.40%	263.45
MOD_097	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3)	24.40%	263.47
MOD_098	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Month, k = 4)	24.40%	263.47
MOD_099	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(DEP_AS_Sin, k = 3)	24.40%	263.49
MOD_100	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(Year, k = 4)	24.30%	263.53
MOD_101	Y ~ 1 + as.factor(Year) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3)	24.30%	263.57
MOD_102	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(DEP, k = 4)	24.30%	263.58
MOD_103	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	24.30%	263.60
MOD_104	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Depth, k = 4) + s(DEP_AS_Sin, k = 3)	24.30%	263.61
MOD_105	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Year, k = 4) + s(Depth, k = 4) + s(DEP_AS_Sin, k = 3)	24.30%	263.61
MOD_106	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4)	24.30%	263.61
MOD_107	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(PAR_STD, k = 4)	24.30%	263.63
MOD_108	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(PAR_STD, k = 4)	24.30%	263.65
MOD_109	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(DEP, k = 4)	24.20%	263.65
MOD_110	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(PAR_STD, k = 4)	24.20%	263.66
MOD_111	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4)	24.20%	263.66
MOD_112	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(SST, k = 4) + s(ZEU, k = 4) + s(CHL, k = 4)	24.20%	263.66
MOD_113	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Year, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	24.20%	263.67
MOD_114	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(DEP, k = 4)	24.20%	263.69
MOD_115	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Year, k = 4) + s(PAR_STD, k = 4)	24.20%	263.74
MOD_116	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4)	24.20%	263.74

Model ID	Model	Dev. Expl.	AIC
MOD_117	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Month, k = 4)	24.20%	263.74
MOD_118	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(Depth, k = 4) + s(DEP_AS_Sin, k = 3)	24.10%	263.75
MOD_119	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(ZEU_STD, k = 4) + s(Month, k = 4)	24.10%	263.75
MOD_120	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	24.10%	263.78
MOD_121	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	24.00%	263.81
MOD_122	Y ~ 1 + s(Speed) + s(Douglas, k = 3) + s(Width_Field, k = 3) + s(Depth, k = 4)	24.00%	263.82
MOD_123	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	24.00%	263.83
MOD_124	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(DEP, k = 4)	24.00%	263.86
MOD_125	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(Month, k = 4)	23.80%	263.96
MOD_126	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	23.80%	263.98
MOD_127	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Depth, k = 4) + s(PAR_STD, k = 4)	23.80%	263.98
MOD_128	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Depth, k = 4)	23.70%	263.99
MOD_129	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Depth, k = 4)	23.70%	264.00
MOD_130	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(PAR, k = 4)	23.70%	264.03
MOD_131	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(PAR, k = 4)	23.70%	264.05
MOD_132	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(PAR, k = 4)	23.60%	264.23
MOD_133	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(DEP, k = 4) + s(Year, k = 4)	23.60%	264.34
MOD_134	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(DEP, k = 4)	23.50%	264.43
MOD_135	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(DEP, k = 4) + s(PAR_STD, k = 4)	23.50%	264.46
MOD_136	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(ZEU_STD, k = 4) + s(Month, k = 4) + s(PAR, k = 4)	23.50%	264.48
MOD_137	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(PAR_STD, k = 4)	23.50%	264.57
MOD_138	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Year, k = 4)	23.50%	264.57
MOD_139	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(PAR, k = 4)	23.40%	264.58
MOD_140	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4)	23.40%	264.58

Model ID	Model	Dev. Expl.	AIC
MOD_141	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4)	23.40%	264.59
MOD_142	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP, k = 4)	23.30%	264.63
MOD_143	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(DEP_AS_Sin, k = 3)	23.30%	264.63
MOD_144	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(ZEU_STD, k = 4)	23.30%	264.63
MOD_145	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(PAR, k = 4)	23.30%	264.64
MOD_146	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Year, k = 4)	23.30%	264.66
MOD_147	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(Month, k = 3)	23.30%	264.68
MOD_148	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Sin, k = 3)	23.30%	264.69
MOD_149	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4)	23.30%	264.73
MOD_150	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	23.30%	264.75
MOD_151	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(PAR_STD, k = 4)	23.10%	264.75
MOD_152	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	23.10%	264.76
MOD_153	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(ZEU_STD, k = 4) + s(PAR, k = 4)	23.10%	264.78
MOD_154	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3)	23.10%	264.82
MOD_155	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(SST, k = 4) + s(ZEU, k = 4) + s(CHL, k = 4) + s(DEP_AS_Cos, k = 3)	23.10%	264.82
MOD_156	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(PAR, k = 4)	23.10%	264.85
MOD_157	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Month, k = 4) + s(DEP_AS_Cos, k = 3)	23.10%	264.85
MOD_158	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(SST, k = 4) + s(ZEU, k = 4) + s(CHL, k = 4) + s(Month, k = 4) + s(DEP_AS_Cos, k = 3)	23.10%	264.85
MOD_159	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(DEP_AS_Sin, k = 3)	23.10%	264.88
MOD_160	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	23.10%	264.92
MOD_161	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(ZEU_STD, k = 4) + s(PAR_STD, k = 4)	23.10%	264.95
MOD_162	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(PAR, k = 4)	23.10%	264.98
MOD_163	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(ZEU_STD, k = 4)	23.10%	265.01
MOD_164	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(DEP, k = 4)	23.00%	265.01
MOD_165	Y ~ 1 + as.factor(Year) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4)	23.00%	265.04

Model ID	Model	Dev. Expl.	AIC
MOD_166	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(Year, k = 4)	23.00%	265.18
MOD_167	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR, k = 4)	23.00%	265.19
MOD_168	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(Year, k = 3)	23.00%	265.29
MOD_169	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(PAR_STD, k = 4)	23.00%	265.29
MOD_170	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Month, k = 4) + s(ZEU_STD, k = 4)	22.90%	265.33
MOD_171	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(DEP_AS_Sin, k = 3)	22.90%	265.36
MOD_172	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(DEP_AS_Sin, k = 3)	22.90%	265.40
MOD_173	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(SST, k = 4) + s(ZEU_STD, k = 4)	22.90%	265.42
MOD_174	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(PAR, k = 4)	22.90%	265.44
MOD_175	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(DEP_AS_Sin, k = 3)	22.90%	265.45
MOD_176	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(DEP, k = 4)	22.80%	265.45
MOD_177	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(PAR_STD, k = 4)	22.80%	265.47
MOD_178	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR_STD, k = 4)	22.80%	265.50
MOD_179	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(ZEU_STD, k = 4)	22.80%	265.55
MOD_180	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4) + s(ZEU_STD, k = 4)	22.80%	265.57
MOD_181	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(PAR_STD, k = 4)	22.80%	265.65
MOD_182	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(PAR, k = 4)	22.80%	265.65
MOD_183	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(ZEU_STD, k = 4) + s(Month, k = 4) + s(PAR_STD, k = 4)	22.70%	265.72
MOD_184	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(PAR, k = 4)	22.70%	265.91
MOD_185	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4)	22.70%	265.92
MOD_186	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(Month, k = 4) + s(PAR_STD, k = 4)	22.70%	265.95
MOD_187	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4) + s(Year, k = 4)	22.60%	266.02
MOD_188	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(Depth, k = 4)	22.60%	266.03
MOD_189	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3)	22.60%	266.05

Model ID	Model	Dev. Expl.	AIC
MOD_190	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(PAR, k = 4)	22.60%	266.10
MOD_191	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(SST, k = 4) + s(ZEU, k = 4) + s(CHL, k = 4) + s(Month, k = 4) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4)	22.60%	266.15
MOD_192	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4)	22.60%	266.23
MOD_193	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4) + s(DEP_AS_Sin, k = 3)	22.50%	266.29
MOD_194	Y ~ 1 + as.factor(Year) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4)	22.50%	266.35
MOD_195	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(PAR, k = 4) + s(DEP, k = 4)	22.50%	266.43
MOD_196	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4) + s(PAR_STD, k = 4)	22.50%	266.46
MOD_197	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 3) + s(CHL, k = 4)	22.50%	266.48
MOD_198	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(DEP_AS_Sin, k = 3)	22.50%	266.48
MOD_199	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Depth, k = 4) + s(PAR, k = 4)	22.40%	266.49
MOD_200	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(DEP, k = 4)	22.40%	266.50
MOD_201	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(PAR, k = 4) + s(DEP_AS_Sin, k = 3)	22.30%	266.53
MOD_202	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Year, k = 4) + s(Depth, k = 4) + s(Month, k = 4) + s(PAR, k = 4)	22.30%	266.64
MOD_203	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(Month, k = 3)	22.30%	266.66
MOD_204	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(PAR_STD, k = 4)	22.30%	266.71
MOD_205	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(PAR, k = 4) + s(PAR_STD, k = 4)	22.30%	266.74
MOD_206	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP, k = 4)	22.20%	266.77
MOD_207	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(DEP_AS_Sin, k = 3)	22.20%	266.82
MOD_208	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(PAR, k = 4)	22.20%	266.91
MOD_209	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(DEP_AS_Sin, k = 3)	22.20%	267.04
MOD_210	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4)	22.20%	267.05
MOD_211	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(PAR, k = 4)	22.20%	267.10
MOD_212	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4)	21.80%	267.12

Model ID	Model	Dev. Expl.	AIC
	+ s(PAR, k = 4)		
MOD_213	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4)	21.80%	267.20
MOD_214	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(DEP_AS_Sin, k = 3)	21.70%	267.30
MOD_215	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(PAR, k = 4) + s(DEP, k = 4)	21.60%	267.31
MOD_216	Y9.4 ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(ZEU_STD, k = 4)	21.60%	267.39
MOD_217	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(PAR, k = 4) + s(DEP_AS_Sin, k = 3)	21.60%	267.40
MOD_218	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(DEP_AS_Sin, k = 3)	21.60%	267.43
MOD_219	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(PAR_STD, k = 4)	21.50%	267.51
MOD_220	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(PAR_STD, k = 4)	21.50%	267.55
MOD_221	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Depth, k = 4) + s(PAR, k = 4)	21.50%	267.58
MOD_222	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(DEP_SL, k = 4)	21.20%	267.60
MOD_223	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(PAR, k = 4) + s(PAR_STD, k = 4)	21.20%	267.63
MOD_224	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(DEP_AS_Sin, k = 3)	21.20%	267.81
MOD_225	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4) + s(Year, k = 4) + s(DEP_AS_Sin, k = 3)	21.20%	267.82
MOD_226	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4) + s(Year, k = 4) + s(PAR_STD, k = 4)	20.90%	267.94
MOD_227	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(DEP, k = 4) + s(PAR, k = 4)	20.90%	268.11
MOD_228	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Sin, k = 3) + s(Month, k = 4) + s(DEP, k = 4) + s(DEP_AS_Cos, k = 3)	20.80%	268.21
MOD_229	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4) + s(Depth, k = 4) + s(PAR, k = 4) + s(ZEU_STD, k = 4) + s(Year, k = 4) + s(PAR_STD, k = 4)	20.50%	268.23
MOD_230	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(SST, k = 4) + s(Month, k = 4)	20.50%	268.32
MOD_231	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(DEP_AS_Cos, k = 3)	20.40%	268.88
MOD_232	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(SST, k = 4) + s(ZEU_STD, k = 4)	20.40%	268.95
MOD_233	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(Depth, k = 4)	20.40%	269.04
MOD_234	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 3) + s(SST, k = 4)	20.20%	269.17

Model ID	Model	Dev. Expl.	AIC
MOD_235	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(DEP, k = 3)	20.20%	269.26
MOD_236	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(ZEU, k = 4) + s(Month, k = 4)	20.10%	269.40
MOD_237	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(ZEU, k = 4)	19.90%	269.97
MOD_238	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(DEP_AS_Sin, k = 3)	19.50%	270.23
MOD_239	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(Year, k = 3)	19.40%	270.70
MOD_240	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 3) + s(ZEU_STD, k = 4)	19.20%	270.91
MOD_241	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(SST, k = 4) + s(ZEU, k = 4)	19.20%	271.03
MOD_242	Y ~ 1 + s(Speed) + s(Douglas, k = 3) + s(Width_Field, k = 3) + s(DEP_SL, k = 4)	19.20%	271.10
MOD_243	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(SST, k = 4) + s(Month, k = 4)	19.10%	271.10
MOD_244	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3)	19.10%	271.31
MOD_245	Y ~ 1 + as.factor(Month) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4)	19.00%	271.63
MOD_246	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(SST, k = 4) + s(ZEU, k = 4)	19.00%	271.94
MOD_247	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(ZEU, k = 4) + s(ZEU_STD, k = 4)	19.00%	271.96
MOD_248	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(SST, k = 4)	19.00%	272.04
MOD_249	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(SST, k = 4) + s(ZEU, k = 4) + s(ZEU_STD, k = 4)	18.80%	272.29
MOD_250	Y ~ 1 + as.factor(Year) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4)	18.70%	272.33
MOD_251	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(Month, k = 3)	18.70%	272.42
MOD_252	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(SST, k = 4) + s(ZEU_STD, k = 4)	18.70%	272.51
MOD_253	Y ~ 1 + as.factor(Year) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4)	18.50%	272.59
MOD_254	Y ~ 1 + as.factor(Month) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3)	18.40%	272.73
MOD_255	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3)	18.40%	272.88
MOD_256	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(SST, k = 4) + s(CHL, k = 4) + s(DEP_AS_Cos, k = 3)	18.30%	272.88
MOD_257	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 3) + s(PAR, k = 4)	18.20%	272.96
MOD_258	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 3) + s(PAR_STD, k = 4)	18.20%	273.02
MOD_259	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 3) + s(ZEU, k = 4)	18.20%	273.05
MOD_260	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(SST, k = 4) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3)	18.20%	273.25
MOD_261	Y ~ 1 + as.factor(Month) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4) + s(SST, k = 4)	18.20%	273.60
MOD_262	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(SST, k = 4) + s(ZEU, k = 4) + s(Month, k = 4)	18.20%	273.78

Model ID	Model	Dev. Expl.	AIC
MOD_263	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(SST, k = 4) + s(Month, k = 4)	18.00%	273.79
MOD_264	Y ~ 1 + s(Speed) + s(Douglas, k = 3) + s(Width_Field, k = 3) + s(SST, k = 4)	17.90%	274.07
MOD_265	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(SST, k = 4) + s(ZEU_STD, k = 4)	17.90%	274.18
MOD_266	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(SST, k = 4)	17.80%	274.60
MOD_267	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(SST, k = 4) + s(DEP_AS_Cos, k = 3)	17.70%	274.72
MOD_268	Y ~ 1 + as.factor(Month) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_SL, k = 4)	17.40%	274.99
MOD_269	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(SST, k = 4) + s(Month, k = 4)	17.30%	275.90
MOD_270	Y ~ 1 + s(Speed) + s(Douglas, k = 3) + s(Width_Field, k = 3) + s(ZEU, k = 4)	17.30%	276.16
MOD_271	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(DEP_AS_Sin, k = 3)	17.30%	276.31
MOD_272	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(DEP_AS_Cos, k = 3)	17.00%	276.87
MOD_273	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(PAR_STD, k = 4)	16.80%	276.98
MOD_274	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(ZEU, k = 4) + s(ZEU_STD, k = 4)	16.70%	277.08
MOD_275	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(ZEU, k = 4) + s(Month, k = 4)	16.60%	277.12
MOD_276	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(Year, k = 3)	16.60%	277.19
MOD_277	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(ZEU, k = 4) + s(DEP_AS_Cos, k = 3)	16.60%	277.26
MOD_278	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(CHL, k = 4)	16.60%	277.78
MOD_279	Y ~ 1 + s(Speed) + s(Douglas, k = 3) + s(Width_Field, k = 3) + s(CHL, k = 4)	16.30%	278.06
MOD_280	Y ~ 1 + as.factor(Year) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3)	16.30%	278.27
MOD_281	Y ~ 1 + s(Speed) + s(Douglas, k = 3) + s(Width_Field, k = 3) + s(DEP_AS_Cos, k = 3)	16.30%	278.32
MOD_282	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4)	16.20%	278.33
MOD_283	Y ~ 1 + s(Speed) + s(Douglas, k = 3) + s(Width_Field, k = 3) + s(DEP_AS_Sin, k = 3)	16.20%	278.43
MOD_284	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(Month, k = 3)	16.20%	278.51
MOD_285	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(Month, k = 4)	16.10%	278.51
MOD_286	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(Year, k = 3)	16.00%	278.66
MOD_287	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(ZEU_STD, k = 4)	16.00%	278.92
MOD_288	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(ZEU_STD, k = 4)	15.80%	278.92
MOD_289	Y ~ 1 + s(Speed) + s(Douglas, k = 3) + s(Width_Field, k = 3) + s(PAR_STD, k = 4)	15.80%	279.04
MOD_290	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(Month, k = 4)	15.80%	279.11

Model ID	Model	Dev. Expl.	AIC
MOD_291	Y ~ 1 + s(Speed) + s(Douglas, k = 3) + s(Width_Field, k = 3) + s(ZEU_STD, k = 4)	15.50%	279.31
MOD_292	Y ~ 1 + as.factor(Month) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4)	15.50%	279.52
MOD_293	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(Month, k = 3)	15.40%	279.56
MOD_294	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(DEP, k = 4)	15.30%	279.63
MOD_295	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(CHL, k = 4) + s(PAR, k = 4)	15.30%	279.74
MOD_296	Y ~ 1 + as.factor(Month) + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3)	15.20%	280.43
MOD_297	Y ~ 1 + s(Speed) + s(Douglas, k = 3) + s(Width_Field, k = 3) + s(PAR, k = 4)	15.00%	280.72
MOD_298	Y ~ 1 + s(Speed) + s(Douglas, k = 3) + s(Width_Field, k = 3) + s(DEP, k = 4)	15.00%	280.92
MOD_299	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(ZEU, k = 4)	14.80%	277.93
MOD_300	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(Month, k = 4)	14.60%	278.54
MOD_301	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(DEP_SL, k = 4) + s(SST, k = 4)	14.30%	264.77
MOD_302	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(DEP_SL, k = 4) + s(CHL, k = 4)	14.20%	265.16
MOD_303	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(DEP_SL, k = 4) + s(ZEU, k = 4)	14.10%	269.56
MOD_304	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(DEP_SL, k = 4) + s(Month, k = 4)	14.00%	268.39
MOD_305	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(SST, k = 4)	13.80%	261.85
MOD_306	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(ZEU, k = 4)	13.70%	264.58
MOD_307	Y ~ 1 + s(Width_Field, k = 3) + s(Speed) + s(Douglas, k = 3) + s(DEP_AS_Cos, k = 3) + s(ZEU_STD, k = 4) + s(DEP_SL, k = 4) + s(CHL, k = 4) + s(Month, k = 4)	13.40%	265.12

Appendix VIII. P-values of the models for the study of the environmental covariate. P-values: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. Covariates abbreviations: sea surface temperature (SST), chlorophyll concentration (CHL), euphotic depth (ZEU), photosynthetically active radiation (PAR), depth (DEP), seabed slope (DEP_SL), seabed aspect (DEP-AS), and their standard deviations (SST-STD, CHL-STD, ZEU-STD, PAR-STD, DEP-STD, DEP_SL-STD, DEP-AS-STD).

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
MOD_001	0.00441 **	2.41e-07 ***	2.25e-12 ***	1.36e-12 ***	< 2e-16 ***	9.61e-10 ***	1.33e-05 ***					8.87e-13 ***	6.22e-13 ***			8.58e-07 ***
MOD_002	0.000580 ***	0.000309 ***	4.96e-11 ***	2.69e-11 ***	< 2e-16 ***	1.02e-11 ***						2.44e-10 ***	9.34e-12 ***			4.45e-05 ***
MOD_003	0.000406 ***	6.05e-05 ***	1.18e-11 ***	1.46e-10 ***	3.60e-16 ***	6.87e-09 ***						7.77e-11 ***	7.18e-12 ***			
MOD_004	0.000279 ***	1.09e-05 ***	2.32e-11 ***	1.58e-12 ***	< 2e-16 ***	2.87e-10 ***		0.000337 ***				1.82e-10 ***	1.82e-12 ***			
MOD_005	0.00294 **	1.81e-05 ***	1.42e-12 ***	2.79e-12 ***	< 2e-16 ***	1.54e-09 ***	2.37e-05 ***				1.17e-09 ***		1.70e-12 ***			1.42e-06 ***
MOD_006	0.00318 **	3.21e-06 ***	2.36e-11 ***	8.90e-11 ***	< 2e-16 ***	1.54e-12 ***						9.83e-10 ***	1.01e-11 ***	0.01016 *		5.72e-05 ***
MOD_007	0.001785 **	5.99e-07 ***	1.29e-12 ***	1.65e-13 ***	< 2e-16 ***	8.58e-08 ***	0.000124 ***	4.43e-05 ***				1.69e-12 ***	1.53e-13 ***			
MOD_008	0.00310 **	5.25e-07 ***	4.97e-12 ***	1.97e-12 ***	< 2e-16 ***	3.73e-05 ***	4.85e-07 ***					6.02e-10 ***	4.48e-13 ***		0.00456 **	6.91e-05 ***
MOD_009	0.0124 *	9.62e-08 ***	1.65e-12 ***	4.40e-12 ***	< 2e-16 ***	4.04e-10 ***	6.84e-05 ***					9.41e-12 ***	1.03e-12 ***	0.0466 *		1.53e-06 ***
MOD_010	0.001495 **	0.000581 ***	3.90e-12 ***	6.14e-12 ***	4.34e-15 ***	0.005581 **	4.46e-06 ***					5.80e-09 ***	6.37e-13 ***		4.74e-05 ***	
MOD_011	0.000435 ***	2.31e-05 ***	2.80e-11 ***	1.74e-11 ***	< 2e-16 ***	2.60e-11 ***					3.72e-07 ***		9.96e-12 ***			6.77e-05 ***
MOD_012	0.00222 **	2.61e-05 ***	5.67e-12 ***	6.60e-10 ***	1.69e-14 ***	1.04e-09 ***						2.86e-10 ***	8.96e-12 ***	0.01068 *		
MOD_013	0.000335 ***	5.39e-06 ***	6.42e-12 ***	3.97e-12 ***	3.09e-15 ***	2.12e-07 ***					6.04e-13 ***		3.62e-12 ***			
MOD_014	0.001841 **	0.000152 ***	8.13e-13 ***	6.04e-11 ***	1.95e-15 ***	7.63e-07 ***	0.000926 ***					1.97e-12 ***	9.16e-13 ***			
MOD_015	0.000173 ***	5.33e-05 ***	6.09e-11 ***	1.10e-10 ***	9.54e-16 ***	6.25e-06 ***						4.30e-08 ***	1.59e-11 ***		0.009290 **	
MOD_016	0.001470 **	0.000188 ***	1.25e-11 ***	9.54e-12 ***	< 2e-16 ***	7.34e-11 ***		0.001162 **				6.39e-10 ***	2.93e-12 ***	0.024655 *		
MOD_017	0.00649 **	1.87e-07 ***	1.96e-12 ***	2.82e-12 ***	< 2e-16 ***	7.09e-10 ***	4.60e-05 ***			0.372		1.31e-11 ***	6.48e-13 ***			9.14e-07 ***

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
MOD_018	0.00153 **	6.06e-06 ***	2.65e-11 ***	7.56e-11 ***	< 2e-16 ***	2.32e-12 ***				0.08658 .		2.00e-09 ***	7.65e-12 ***			3.78e-05 ***
MOD_019	0.00436 **	2.39e-07 ***	2.59e-12 ***	1.76e-12 ***	< 2e-16 ***	1.51e-09 ***	2.19e-05 ***		0.76332			8.91e-13 ***	1.88e-12 ***			9.10e-07 ***
MOD_020	0.000614 ***	9.63e-06 ***	5.24e-11 ***	4.02e-11 ***	< 2e-16 ***	7.53e-12 ***			0.308603			1.86e-10 ***	1.82e-11 ***			2.61e-05 ***
MOD_021	0.000378 ***	1.49e-05 ***	8.83e-11 ***	6.25e-11 ***	< 2e-16 ***	1.53e-08 ***						9.59e-09 ***	1.31e-11 ***		0.271592	0.000786 ***
MOD_022	0.000206 ***	7.96e-07 ***	1.22e-11 ***	2.61e-13 ***	< 2e-16 ***	6.28e-08 ***		0.002258 **			8.38e-12 ***		1.36e-12 ***			
MOD_023	0.005626 **	0.000409 ***	2.81e-12 ***	1.56e-11 ***	2.87e-11 ***	0.002399 **	1.60e-05 ***					5.93e-08 ***	8.15e-13 ***	0.025772 *	2.16e-05 ***	
MOD_024	0.009995 **	2.01e-07 ***	3.53e-12 ***	4.38e-12 ***	1.74e-15 ***	1.98e-05 ***	1.76e-06 ***					8.58e-09 ***	5.98e-13 ***	0.032831 *	0.002117 **	0.000136 ***
MOD_025	0.001949 **	0.000192 ***	3.59e-12 ***	2.88e-12 ***	< 2e-16 ***	7.68e-05 ***	1.06e-06 ***				1.39e-05 ***		6.78e-13 ***		0.002684 **	0.000137 ***
MOD_026	0.000984 ***	4.19e-05 ***	6.29e-12 ***	4.17e-10 ***	2.81e-14 ***	1.79e-09 ***				0.097783 .		7.05e-10 ***	5.74e-12 ***			
MOD_027	0.001417 **	1.64e-06 ***	3.34e-12 ***	5.82e-13 ***	< 2e-16 ***	0.000475 ***	4.62e-06 ***	0.007343 **				1.01e-09 ***	2.14e-13 ***		0.005369 **	
MOD_028	0.001201 **	0.000901 ***	3.09e-11 ***	3.71e-10 ***	3.33e-14 ***	7.87e-07 ***						2.57e-07 ***	1.40e-11 ***	0.005998 **	0.003959 **	
MOD_029	0.001156 **	1.45e-05 ***	8.25e-13 ***	3.21e-13 ***	< 2e-16 ***	1.31e-07 ***	0.000241 ***	8.50e-05 ***			7.03e-09 ***		3.05e-13 ***			
MOD_030	8.58e-05 ***	1.22e-06 ***	3.45e-11 ***	5.77e-12 ***	2.22e-16 ***	0.000149 ***					8.12e-10 ***		1.49e-12 ***		0.000143 ***	
MOD_031	0.00219 **	1.75e-05 ***	1.52e-11 ***	8.54e-11 ***	< 2e-16 ***	4.44e-12 ***					5.95e-07 ***		1.37e-11 ***	0.01461 *		7.12e-05 ***
MOD_032	0.000400 ***	6.64e-05 ***	1.14e-11 ***	1.09e-10 ***	2.66e-16 ***	1.17e-08 ***					0.793897	0.002665 **	4.21e-11 ***			
MOD_033	0.00804 **	1.68e-05 ***	1.13e-12 ***	1.27e-11 ***	< 2e-16 ***	6.33e-10 ***	9.83e-05 ***				4.03e-09 ***		3.32e-12 ***	0.05700 .		2.04e-06 ***
MOD_034	0.002405 **	0.000202 ***	2.47e-13 ***	1.65e-08 ***	2.59e-09 ***		7.07e-06 ***					3.37e-11 ***	< 2e-16 ***			
MOD_035	0.000411 ***	6.12e-05 ***	1.20e-11 ***	1.92e-10 ***	5.42e-16 ***	8.10e-09 ***			0.969331			8.37e-11 ***	5.35e-11 ***			
MOD_036	0.005025 **	3.64e-07 ***	1.04e-12 ***	8.41e-13 ***	2.60e-16 ***	4.78e-08 ***	0.000454 ***	0.000148 ***				1.30e-11 ***	3.19e-13 ***	0.087680 .		
MOD_037	0.000308	0.000659	7.43e-12	5.96e-08	1.53e-11							3.59e-09	< 2e-16			

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
	***	***	***	***	***							***	***			
MOD_038	0.00574 **	8.56e-06 ***	6.19e-13 ***	2.32e-10 ***	1.22e-11 ***	2.58e-07 ***	0.00350 **					1.63e-11 ***	1.56e-12 ***	0.03752 *		
MOD_039	0.000278 ***	3.21e-05 ***	2.41e-11 ***	1.27e-12 ***	< 2e-16 ***	4.57e-10 ***		0.000333 ***			0.864992	0.001957 **	4.19e-11 ***			
MOD_040	0.000189 ***	1.54e-05 ***	4.81e-11 ***	9.31e-12 ***	< 2e-16 ***	1.26e-07 ***		0.007435 **				8.41e-09 ***	4.42e-12 ***		0.26784	
MOD_041	0.000633 ***	7.38e-06 ***	1.49e-11 ***	4.83e-12 ***	2.23e-16 ***	1.07e-10 ***		0.000540 ***		0.174261		1.06e-09 ***	1.65e-12 ***			
MOD_042	0.00151 **	3.85e-05 ***	4.13e-12 ***	4.38e-10 ***	5.17e-15 ***	2.75e-09 ***					5.10e-07 ***		5.69e-12 ***	0.01773 *		
MOD_043	0.000285 ***	1.05e-05 ***	2.35e-11 ***	2.01e-12 ***	< 2e-16 ***	3.32e-10 ***		0.000325 ***	0.738612			1.75e-10 ***	8.98e-12 ***			
MOD_044	0.0155 *	2.18e-05 ***	1.46e-12 ***	1.27e-11 ***	< 2e-16 ***	2.34e-10 ***	3.71e-05 ***				0.2467	8.66e-05 ***	1.09e-10 ***	0.0389 *		8.76e-07 ***
MOD_045	0.001987 **	2.57e-05 ***	1.22e-12 ***	2.45e-13 ***	< 2e-16 ***	6.64e-08 ***	9.34e-05 ***	3.12e-05 ***			0.44744	0.000199 ***	1.16e-11 ***			
MOD_046	0.00339 **	1.31e-05 ***	4.83e-12 ***	3.57e-12 ***	< 2e-16 ***	3.12e-05 ***	4.35e-07 ***				0.54947	0.00120 **	4.07e-11 ***		0.00599 **	5.78e-05 ***
MOD_047	0.00210 **	4.72e-06 ***	4.53e-11 ***	1.94e-10 ***	< 2e-16 ***	2.76e-09 ***						7.23e-08 ***	1.22e-11 ***	0.00736 **	0.14546	0.00143 **
MOD_048	0.00210 **	4.72e-06 ***	4.53e-11 ***	1.94e-10 ***	< 2e-16 ***	2.76e-09 ***						7.23e-08 ***	1.22e-11 ***	0.00736 **	0.14546	0.00143 **
MOD_049	0.00431 **	1.66e-05 ***	1.25e-12 ***	5.91e-12 ***	< 2e-16 ***	1.09e-09 ***	7.51e-05 ***			0.38164	1.02e-08 ***		1.96e-12 ***			1.43e-06 ***
MOD_050	0.00468 **	4.11e-07 ***	4.30e-12 ***	3.02e-12 ***	5.53e-16 ***	2.39e-05 ***	1.73e-06 ***			0.37644		5.81e-09 ***	5.00e-13 ***		0.00463 **	7.27e-05 ***
MOD_051	0.00313 **	3.22e-06 ***	2.52e-11 ***	1.16e-10 ***	< 2e-16 ***	1.60e-12 ***			0.65658			9.18e-10 ***	1.63e-11 ***	0.01802 *		5.83e-05 ***
MOD_052	0.00294 **	1.85e-05 ***	1.57e-12 ***	3.66e-12 ***	< 2e-16 ***	2.66e-09 ***	3.26e-05 ***		0.90089		1.09e-09 ***		4.48e-12 ***			1.75e-06 ***
MOD_053	0.001846 **	5.94e-07 ***	1.26e-12 ***	1.91e-13 ***	< 2e-16 ***	1.91e-07 ***	0.000123 ***	5.03e-05 ***	0.696288			1.73e-12 ***	1.04e-12 ***			
MOD_054	0.002359 **	5.38e-07 ***	1.27e-12 ***	3.41e-13 ***	2.42e-16 ***	8.16e-08 ***	0.000298 ***	5.95e-05 ***		0.5526		1.47e-11 ***	1.60e-13 ***			
MOD_055	0.00110 **	1.80e-05 ***	1.56e-11 ***	5.49e-11 ***	< 2e-16 ***	6.46e-12 ***				0.09783 .	1.75e-06 ***		1.01e-11 ***			5.29e-05 ***
MOD_056	0.003110 **	5.35e-12 ***	5.35e-12 ***	1.97e-12 ***	< 2e-16 ***	7.00e-05 ***	8.61e-07 ***		0.994848			6.18e-10 ***	1.60e-12 ***		0.004855 **	0.000101 ***

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
MOD_057	0.001464 **	0.000851 ***	3.95e-12 ***	4.68e-12 ***	3.56e-15 ***	0.006224 **	5.39e-06 ***				0.921474	0.007936 **	6.87e-12 ***		4.81e-05 ***	
MOD_058	0.00100 **	1.83e-05 ***	7.84e-12 ***	9.37e-12 ***	< 2e-16 ***	1.85e-10 ***		0.00152 **			5.67e-07 ***		3.47e-12 ***	0.03331 *		
MOD_059	5.51e-05 ***	1.36e-05 ***	2.95e-11 ***	1.37e-09 ***	2.28e-15 ***	0.000851 ***							5.02e-08 ***		3.42e-06 ***	
MOD_060	0.0125 *	9.64e-08 ***	1.77e-12 ***	5.32e-12 ***	< 2e-16 ***	6.38e-10 ***	7.60e-05 ***		0.9884			9.93e-12 ***	2.33e-12 ***	0.0532 .		2.28e-06 ***
MOD_061	0.00233 **	1.12e-05 ***	3.29e-12 ***	9.31e-12 ***	3.18e-13 ***	0.00339 **	1.61e-05 ***			0.32912		5.09e-08 ***	7.08e-13 ***		5.01e-05 ***	
MOD_062	0.000524 ***	8.16e-07 ***	2.10e-11 ***	1.83e-11 ***	5.26e-15 ***	3.05e-05 ***					1.70e-07 ***		1.38e-12 ***	0.012673 *	3.90e-05 ***	
MOD_063	0.001558 **	0.000562 ***	3.42e-12 ***	7.60e-12 ***	4.41e-15 ***	0.011928 *	3.34e-06 ***		0.36259			6.21e-09 ***	5.18e-12 ***		3.72e-05 ***	
MOD_064	0.000635 ***	0.000627 ***	2.32e-12 ***	5.57e-11 ***	1.72e-15 ***	0.134671	4.73e-05 ***						3.08e-09 ***		4.16e-09 ***	
MOD_065	0.000117 ***	2.38e-07 ***	4.88e-11 ***	1.16e-11 ***	< 2e-16 ***	2.24e-06 ***					2.16e-09 ***		3.34e-12 ***		0.010390 *	0.005015 **
MOD_066	0.000456 ***	2.44e-05 ***	2.90e-11 ***	2.88e-11 ***	< 2e-16 ***	2.18e-11 ***			0.428987		1.96e-07 ***		2.16e-11 ***			4.88e-05 ***
MOD_067	0.00227 **	5.66e-05 ***	5.81e-12 ***	7.54e-10 ***	2.17e-14 ***	1.61e-09 ***					0.85025	0.00156 **	5.72e-11 ***	0.01112 *		
MOD_068	0.001881 **	6.27e-05 ***	8.03e-13 ***	5.43e-11 ***	2.00e-15 ***	8.58e-07 ***	0.000974 ***				0.859189	0.000615 ***	1.16e-11 ***			
MOD_069	0.000483 ***	3.75e-05 ***	3.33e-11 ***	2.67e-10 ***	3.65e-14 ***	1.33e-06 ***				0.077502 .		3.73e-07 ***	1.35e-11 ***		0.007258 **	
MOD_070	0.002808 **	0.000130 ***	6.83e-13 ***	1.11e-10 ***	7.77e-12 ***	4.70e-07 ***	0.002695 **			0.304952		3.07e-11 ***	9.14e-13 ***			
MOD_071	0.001910 **	0.000146 ***	7.91e-13 ***	7.99e-11 ***	2.50e-15 ***	1.49e-06 ***	0.000773 ***		0.551778			2.13e-12 ***	8.71e-12 ***			
MOD_072	0.006177 **	0.000184 ***	2.72e-12 ***	8.45e-12 ***	7.87e-16 ***	4.16e-05 ***	3.20e-06 ***				6.46e-05 ***		1.11e-12 ***	0.039479 *	0.001230 **	0.000228 ***
MOD_073	0.000896 ***	0.000193 ***	2.53e-12 ***	5.38e-13 ***	< 2e-16 ***	0.001064 **	9.55e-06 ***	0.015335 *			5.19e-05 ***		2.27e-13 ***		0.002545 **	
MOD_074	0.004838 **	9.86e-07 ***	2.61e-12 ***	2.62e-12 ***	2.62e-14 ***	0.000347 ***	1.19e-05 ***	0.023116 *				1.39e-08 ***	3.41e-13 ***	0.049371 *	0.001914 **	
MOD_075	0.000717 ***	0.000273 ***	4.24e-12 ***	2.15e-10 ***	1.12e-14 ***	4.30e-09 ***				0.11967	1.60e-06 ***		3.25e-12 ***			
MOD_076	0.000164	0.001081	5.76e-11	7.54e-11	5.66e-16	1.02e-05					0.592369	0.018223	5.13e-11		0.008495	

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP _sin	DEP_ASP _cos	DEP_SL	Depth	YEAR	MONTH
	***	**	***	***	***	***						*	***		**	
MOD_077	0.000494 ***	0.000685 ***	1.51e-11 ***	2.82e-09 ***	6.23e-14 ***	8.93e-05 ***							4.91e-09 ***	0.002700 **	8.91e-07 ***	
MOD_078	0.000177 ***	5.34e-05 ***	6.14e-11 ***	1.45e-10 ***	1.55e-15 ***	6.65e-06 ***			0.904395			4.35e-08 ***	8.23e-11 ***		0.009230 **	
MOD_079	7.34e-05 ***	1.04e-05 ***	3.69e-11 ***		< 2e-16 ***	4.53e-10 ***						6.03e-08 ***	1.64e-13 ***			4.86e-06 ***
MOD_080	0.00105 **	7.79e-06 ***	2.92e-11 ***	6.27e-11 ***	5.77e-15 ***	5.09e-08 ***		0.03303 *				7.46e-08 ***	5.82e-12 ***	0.01486 *	0.1112	
MOD_081	0.000316 ***	4.29e-05 ***	8.28e-12 ***	6.68e-11 ***	< 2e-16 ***	5.47e-07 ***			0.84478		7.00e-07 ***		2.65e-11 ***			
MOD_082	0.00346 **	6.17e-06 ***	1.46e-12 ***	1.03e-10 ***	9.59e-11 ***	0.04964 *	8.64e-05 ***						4.51e-10 ***	0.00712 **	1.41e-09 ***	
MOD_083	0.003128 **	1.58e-05 ***	7.23e-13 ***	2.06e-12 ***	6.60e-16 ***	7.11e-08 ***	0.000733 ***	0.000215 ***			1.83e-08 ***		7.17e-13 ***	0.102623		
MOD_084	0.00364 **	3.43e-05 ***	5.21e-13 ***	2.02e-10 ***	1.26e-13 ***	4.94e-07 ***	0.00530 **				7.61e-08 ***		1.34e-12 ***	0.05244 .		
MOD_085	0.000128 ***	1.24e-05 ***	3.04e-11 ***	6.39e-12 ***	< 2e-16 ***	4.50e-07 ***		0.015347 *			5.61e-05 ***		2.91e-12 ***		0.164861	
MOD_086	0.000460 ***	1.75e-05 ***	8.40e-12 ***	3.99e-12 ***	< 2e-16 ***	2.52e-10 ***		0.000827 ***		0.188789	1.32e-06 ***		1.92e-12 ***			
MOD_087	0.000326 ***	2.70e-05 ***	1.70e-12 ***	1.42e-08 ***	< 2e-16 ***	6.37e-07 ***							5.65e-07 ***			
MOD_088	0.000326 ***	0.000241 ***	1.70e-12 ***	1.42e-08 ***	< 2e-16 ***	6.37e-07 ***							5.65e-07 ***			
MOD_089	0.000213 ***	2.03e-05 ***	1.30e-11 ***	1.55e-12 ***	< 2e-16 ***	8.14e-10 ***		0.000611 ***	0.902619		3.22e-07 ***		8.07e-12 ***			
MOD_090	0.01187 *	1.08e-05 ***	3.27e-12 ***	1.27e-11 ***	1.06e-15 ***	1.31e-05 ***	1.27e-06 ***				0.38039	0.00101 **	5.67e-11 ***	0.02907 *	0.00303 **	9.21e-05 ***
MOD_091	0.01187 *	1.08e-05 ***	3.27e-12 ***	1.27e-11 ***	1.09e-15 ***	1.31e-05 ***	1.27e-06 ***				0.38039	0.00101 **	5.67e-11 ***	0.02907 *	0.00303 **	9.21e-05 ***
MOD_092	0.000104 ***	0.000146 ***	3.15e-12 ***	3.16e-10 ***	< 2e-16 ***	3.66e-08 ***		0.000124 ***					7.32e-08 ***			
MOD_093	0.000112 ***	8.20e-05 ***	2.14e-13 ***		8.31e-06 ***									8.29e-12 ***		
MOD_094	0.00613 **	4.92e-06 ***	2.36e-12 ***	1.59e-11 ***	1.43e-12 ***	0.00491 **	8.58e-06 ***		0.21717			6.89e-08 ***	4.67e-12 ***	0.01627 *	1.59e-05 ***	
MOD_095	0.00580 **	2.06e-05 ***	2.82e-12 ***	1.86e-11 ***	9.26e-13 ***	0.00239 **	1.58e-05 ***				0.80094	0.00653 **	1.21e-11 ***	0.02573 *	2.34e-05 ***	

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
MOD_096	0.000248 ***	1.04e-06 ***	1.96e-11 ***	1.31e-11 ***	1.12e-14 ***	3.26e-05 ***				0.070864 .	5.70e-08 ***		1.58e-12 ***		0.000103 ***	
MOD_097	1.99e-05 ***	2.90e-05 ***	3.55e-12 ***		2.81e-16 ***	6.09e-08 ***						1.39e-08 ***	6.62e-14 ***			
MOD_098	6.04e-05 ***	7.77e-06 ***	4.47e-11 ***	4.70e-09 ***	< 2e-16 ***	1.25e-05 ***							5.95e-08 ***		0.000995 ***	0.003090 **
MOD_099	0.001480 **	1.55e-05 ***	3.26e-12 ***	6.88e-13 ***	< 2e-16 ***	0.000434 ***	4.48e-06 ***	0.006323 **			0.674038	0.002150 **	9.29e-12 ***		0.006962 **	
MOD_100	0.001321 **	8.94e-06 ***	3.12e-11 ***	1.41e-10 ***	< 2e-16 ***	1.07e-08 ***					0.000133 ***		1.17e-11 ***	0.010823 *	0.098601 .	0.002145 **
MOD_101	1.15e-05 ***	6.19e-05 ***	5.62e-10 ***	0.000133 ***	< 2e-16 ***	8.34e-05 ***						8.90e-11 ***	9.61e-14 ***			
MOD_102	0.002978 **	3.35e-06 ***	3.10e-12 ***	4.80e-12 ***	4.78e-16 ***	4.85e-05 ***	3.35e-06 ***			0.368412	6.02e-05 ***		9.00e-13 ***		0.002697 **	0.000139 ***
MOD_103	0.010171 *	5.78e-05 ***	3.52e-12 ***	4.49e-12 ***	1.10e-15 ***	4.20e-05 ***	1.94e-06 ***		0.76446			9.57e-09 ***	1.66e-12 ***	0.032785 *	0.002031 **	0.000278 ***
MOD_104	0.005955 **	2.61e-05 ***	9.54e-13 ***	1.86e-12 ***	2.65e-15 ***	3.06e-08 ***	0.000292 ***	8.98e-05 ***			0.332544	0.000166 ***	2.14e-11 ***	0.077763 .		
MOD_105	0.00119 **	2.98e-05 ***	3.09e-11 ***	3.59e-10 ***	3.33e-14 ***	1.23e-06 ***					0.94972	0.01265 *	6.07e-11 ***	0.00680 **	0.00404 **	
MOD_106	0.000756 ***	3.50e-06 ***	1.11e-11 ***		5.53e-15 ***	1.12e-10 ***						1.84e-07 ***	4.33e-13 ***	0.013318 *		7.56e-06 ***
MOD_107	0.001964 **	0.000192 ***	3.73e-12 ***	2.93e-12 ***	< 2e-16 ***	0.000160 ***	1.48e-06 ***		0.866476		1.46e-05 ***		1.99e-12 ***		0.002685 **	0.000231 ***
MOD_108	0.00147 **	1.72e-06 ***	3.09e-12 ***	6.31e-13 ***	< 2e-16 ***	0.00113 **	4.60e-06 ***	0.00970 **	0.54494			1.09e-09 ***	1.57e-12 ***		0.00483 **	
MOD_109	0.001997 **	1.48e-06 ***	3.15e-12 ***	8.91e-13 ***	8.04e-14 ***	0.000358 ***	1.22e-05 ***	0.009330 **		0.487875		7.80e-09 ***	2.40e-13 ***		0.005038 **	
MOD_110	0.001209 **	1.40e-05 ***	7.91e-13 ***	3.70e-13 ***	< 2e-16 ***	3.11e-07 ***	0.000213 ***	0.000102 ***	0.581187		8.74e-09 ***		1.57e-12 ***			
MOD_111	0.000513 ***	8.21e-06 ***	1.99e-11 ***	1.48e-13 ***	2.44e-15 ***	< 2e-16 ***										
MOD_112	0.000513 ***	8.21e-06 ***	1.99e-11 ***	1.48e-13 ***	2.44e-15 ***	< 2e-16 ***										
MOD_113	0.00122 **	2.25e-05 ***	3.14e-11 ***	4.38e-10 ***	6.05e-14 ***	8.77e-07 ***			0.65028			2.91e-07 ***	5.30e-11 ***	0.00597 **	0.00421 **	
MOD_114	0.001532 **	1.47e-05 ***	8.14e-13 ***	6.97e-13 ***	2.29e-16 ***	1.14e-07 ***	0.000536 ***	0.000105 ***		0.550199	3.16e-08 ***		3.52e-13 ***			
MOD_115	8.58e-05	1.23e-06	3.55e-11	7.43e-12	2.50e-16	0.000170			0.831519		8.70e-10		6.33e-12		0.000155	

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
	***	***	***	***	***	***					***		*		***	
MOD_116	0.000529 ***	6.45e-07 ***	2.58e-12 ***		< 2e-16 ***	3.93e-07 ***	0.000724 ***					2.35e-09 ***	2.70e-14 ***			1.23e-06 ***
MOD_117	0.000428 ***	0.000329 ***	1.10e-10 ***	1.30e-12 ***	< 2e-16 ***	< 2e-16 ***										0.000117 ***
MOD_118	0.006122 **	6.02e-05 ***	6.05e-13 ***	3.22e-10 ***	4.85e-13 ***	2.43e-07 ***	0.003096 **				0.618641	0.000457 ***	2.11e-11 ***	0.034938 *		
MOD_119	0.003584 **	1.89e-06 ***	1.83e-12 ***	2.45e-10 ***	1.31e-13 ***	0.002515 **	1.77e-05 ***						4.96e-10 ***	0.007066 **	4.46e-07 ***	0.000845 ***
MOD_120	0.008203 **	1.64e-05 ***	1.18e-12 ***	1.50e-11 ***	< 2e-16 ***	1.11e-09 ***	0.000101 ***		0.860959		4.51e-09 ***		6.79e-12 ***	0.059644 .		3.51e-06 ***
MOD_121	0.00631 **	7.05e-06 ***	5.74e-13 ***	2.49e-10 ***	7.22e-13 ***	4.26e-07 ***	0.00241 **		0.32935			2.15e-11 ***	9.46e-12 ***	0.02621 *		
MOD_122	0.00373 **	3.77e-07 ***	3.65e-15 ***											7.94e-14 ***		
MOD_123	0.005423 **	3.22e-07 ***	9.68e-13 ***	8.89e-13 ***	8.18e-15 ***	8.88e-08 ***	0.000369 ***	0.000204 ***	0.519787			1.52e-11 ***	1.47e-12 ***	0.073033 .		
MOD_124	0.000227 ***	1.19e-05 ***	1.31e-11 ***	1.93e-09 ***	3.75e-13 ***	6.60e-05 ***				0.009808 **			1.07e-08 ***		2.93e-06 ***	
MOD_125	0.000521 ***	4.47e-06 ***	2.30e-11 ***	9.38e-09 ***	1.10e-15 ***	1.40e-06 ***							5.79e-09 ***	0.002800 **	0.000336 ***	0.004538 **
MOD_126	0.002107 **	1.15e-06 ***	2.59e-11 ***	1.42e-11 ***	< 2e-16 ***	3.67e-08 ***			0.808893		5.93e-10 ***		9.25e-12 ***	0.035575 *		0.000207 ***
MOD_127	0.00157 **	3.33e-05 ***	4.36e-12 ***	4.19e-10 ***	1.09e-14 ***	3.54e-09 ***			0.46734		1.08e-06 ***		2.31e-11 ***	0.01456 *		
MOD_128	0.00156 **	2.33e-05 ***	8.55e-13 ***	4.07e-08 ***	7.54e-14 ***	9.31e-08 ***							7.89e-08 ***	0.00693 **		
MOD_129	0.000264 ***	2.69e-05 ***	1.17e-12 ***		2.77e-12 ***	2.05e-08 ***						4.15e-08 ***	2.44e-13 ***	0.013847 *		
MOD_130	3.80e-05 ***	0.000533 ***	2.46e-11 ***	6.19e-10 ***	< 2e-16 ***	0.000105 ***		0.045861 *					2.56e-08 ***		0.000722 ***	
MOD_131	0.230366	1.37e-06 ***	4.51e-12 ***	6.01e-09 ***	3.86e-10 ***	2.30e-06 ***	2.28e-09 ***	3.37e-09 ***				4.48e-06 ***	1.04e-10 ***	0.000504 ***	2.60e-09 ***	2.57e-10 ***
MOD_132	4.45e-05 ***	1.47e-05 ***	4.78e-11 ***		< 2e-16 ***	2.74e-10 ***		0.0125 *				1.09e-08 ***	5.19e-13 ***			3.45e-05 ***
MOD_133	0.000666 ***	1.02e-05 ***	3.08e-11 ***	9.61e-11 ***	< 2e-16 ***	1.08e-08 ***				0.087302 .	0.000198 ***		1.06e-11 ***		0.156656	0.001290 **
MOD_134	0.000348 ***	5.94e-06 ***	1.28e-11 ***		9.76e-14 ***	6.73e-11 ***				0.035976 *		3.39e-07 ***	1.00e-13 ***			3.16e-06 ***

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
MOD_135	0.00108 **	1.91e-05 ***	1.70e-11 ***	6.65e-11 ***	< 2e-16 ***	6.62e-12 ***			0.68663	0.12484	1.21e-06 ***		2.63e-11 ***			5.43e-05 ***
MOD_136	0.14547	2.21e-06 ***	2.77e-12 ***	1.59e-10 ***	5.62e-11 ***	4.96e-05 ***	5.23e-09 ***	9.98e-10 ***					1.33e-08 ***	0.000114 ***	2.41e-13 ***	5.11e-11 ***
MOD_137	5.56e-05 ***	1.38e-05 ***	3.05e-11 ***	2.11e-09 ***	1.85e-15 ***	0.000902 ***			0.889436				1.50e-07 ***		3.68e-06 ***	
MOD_138	1.10e-05 ***	0.000187 ***	1.22e-11 ***		1.93e-15 ***	0.000195 ***						1.81e-06 ***	6.14e-14 ***		0.006837 **	
MOD_139	0.0315 *	7.56e-06 ***	1.06e-11 ***	5.18e-07 ***	< 2e-16 ***	6.28e-05 ***	1.66e-09 ***	1.28e-07 ***				2.13e-07 ***	1.26e-10 ***		1.23e-07 ***	4.00e-09 ***
MOD_140	0.000112 ***	9.45e-06 ***	3.28e-13 ***		1.88e-13 ***	1.51e-05 ***	0.003655 **					7.78e-10 ***	1.26e-14 ***			
MOD_141	0.000611 ***	5.29e-06 ***	1.19e-11 ***		1.56e-12 ***	3.44e-11 ***		0.005222 **				2.39e-08 ***	9.31e-13 ***	0.004718 **		2.36e-05 ***
MOD_142	0.000876 ***	2.59e-05 ***	6.66e-13 ***	2.74e-08 ***	5.59e-11 ***	4.92e-08 ***				0.010702 *			1.02e-07 ***			
MOD_143	0.005320 **	1.47e-05 ***	2.49e-12 ***	3.74e-12 ***	3.99e-13 ***	0.000272 ***	1.00e-05 ***	0.017564 *			0.520455	0.002150 **	1.54e-11 ***	0.046579 *	0.002705 **	
MOD_144	0.00266 **	4.90e-07 ***	1.23e-12 ***		4.59e-13 ***	1.98e-07 ***	0.00293 **					1.49e-08 ***	7.82e-14 ***	0.05312 .		2.13e-06 ***
MOD_145	0.000355 ***	6.12e-06 ***	1.43e-11 ***	1.92e-09 ***	8.42e-14 ***	2.40e-05 ***		0.139276					3.46e-09 ***	0.004814 **	0.000141 ***	
MOD_146	3.89e-05 ***	4.30e-05 ***	5.96e-11 ***		< 2e-16 ***	1.06e-06 ***						1.04e-06 ***	1.30e-13 ***		0.107	4.71e-05 ***
MOD_147	5.48e-06 ***	2.86e-06 ***	7.47e-12 ***		< 2e-16 ***	3.07e-08 ***							3.11e-10 ***			9.77e-07 ***
MOD_148	1.38e-05 ***	1.17e-05 ***	2.02e-12 ***		< 2e-16 ***	2.39e-05 ***					0.000112 ***		1.08e-13 ***			
MOD_149	0.00038 ***	5.77e-06 ***	3.61e-12 ***		4.81e-15 ***	0.00219 **	4.26e-05 ***					1.30e-07 ***	8.60e-15 ***		0.00477 **	1.58e-05 ***
MOD_150	0.00523 **	9.20e-07 ***	2.30e-12 ***	2.53e-12 ***	1.43e-12 ***	0.00084 ***	8.49e-06 ***	0.03648 *	0.36778			1.72e-08 ***	1.86e-12 ***	0.03667 *	0.00154 **	
MOD_151	8.14e-05 ***	9.63e-06 ***	3.13e-11 ***		< 2e-16 ***	2.42e-10 ***			0.212			3.22e-08 ***	5.85e-13 ***			2.43e-06 ***
MOD_152	0.006296 **	0.000173 ***	2.68e-12 ***	8.54e-12 ***	2.00e-15 ***	9.79e-05 ***	3.13e-06 ***		0.646351		8.13e-05 ***		2.67e-12 ***	0.036468 *	0.001099 **	0.000531 ***
MOD_153	0.002505 **	0.000364 ***	1.35e-12 ***	7.88e-11 ***	2.19e-11 ***	0.021123 *	8.11e-05 ***	0.128439					3.17e-10 ***	0.010599 *	2.76e-07 ***	
MOD_154	0.000701	0.001061	6.29e-11	1.65e-14	1.97e-14	< 2e-16						0.016931				

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
	***	**	***	***	***	***						*				
MOD_155	0.000701 ***	1.13e-05 ***	6.29e-11 ***	1.65e-14 ***	1.97e-14 ***	< 2e-16 ***						0.016931 *				
MOD_156	0.000295 ***	3.15e-06 ***	2.52e-12 ***		1.96e-15 ***	1.30e-07 ***	0.000416 ***	0.008557 **				2.91e-10 ***	7.13e-14 ***			1.98e-05 ***
MOD_157	0.000804 ***	0.000599 ***	3.21e-10 ***	1.79e-13 ***	< 2e-16 ***	< 2e-16 ***						0.013043 *				0.000109 ***
MOD_158	0.000804 ***	0.000599 ***	3.21e-10 ***	1.79e-13 ***	< 2e-16 ***	5.14e-16 ***						0.013043 *				0.000109 ***
MOD_159	8.02e-05 ***	5.98e-05 ***	5.21e-11 ***		< 2e-16 ***	4.72e-10 ***					0.350464	0.000529 ***	2.04e-11 ***			3.32e-06 ***
MOD_160	0.000491 ***	0.000650 ***	1.70e-11 ***	4.65e-09 ***	7.49e-14 ***	8.90e-05 ***			0.484035				1.64e-08 ***	0.002340 **	1.23e-06 ***	
MOD_161	0.00356 **	5.22e-06 ***	1.32e-12 ***	2.04e-10 ***	2.60e-12 ***	0.07141 .	4.26e-05 ***		0.17321				2.24e-09 ***	0.00419 **	1.23e-09 ***	
MOD_162	0.19478	4.99e-05 ***	3.78e-12 ***	1.48e-09 ***	1.68e-10 ***	8.78e-06 ***	3.06e-09 ***	1.41e-09 ***			0.01441 *		1.56e-10 ***	0.00055 ***	1.56e-10 ***	1.24e-10 ***
MOD_163	0.000953 ***	2.66e-05 ***	4.71e-13 ***	1.06e-08 ***	6.71e-16 ***	1.75e-05 ***	0.086560 .						3.08e-07 ***			
MOD_164	7.88e-05 ***	1.85e-05 ***	1.44e-12 ***		1.68e-11 ***	1.61e-08 ***				0.0585 .		9.72e-08 ***	4.54e-14 ***			
MOD_165	2.51e-06 ***	4.28e-06 ***	4.18e-10 ***		7.69e-15 ***	0.059 .							2.64e-09 ***			
MOD_166	0.000462 ***	2.56e-05 ***	1.85e-11 ***		5.65e-14 ***	3.48e-07 ***						4.58e-06 ***	2.83e-13 ***	0.010653 *	0.062012 .	9.20e-05 ***
MOD_167	2.41e-05 ***	3.77e-05 ***	7.00e-12 ***		< 2e-16 ***	2.19e-08 ***		0.13				6.66e-08 ***	5.63e-14 ***			
MOD_168	1.44e-06 ***	8.64e-05 ***	5.25e-12 ***		< 2e-16 ***	0.00935 **							1.67e-11 ***		1.58e-05 ***	
MOD_169	0.000318 ***	2.73e-05 ***	1.96e-12 ***	2.87e-08 ***	< 2e-16 ***	6.89e-07 ***			0.654626				2.05e-06 ***			
MOD_170	0.000825 ***	3.08e-06 ***	3.53e-11 ***	5.68e-13 ***	< 2e-16 ***	< 2e-16 ***	0.060696 .									3.22e-05 ***
MOD_171	0.001060 **	4.50e-05 ***	1.48e-11 ***		7.43e-16 ***	6.29e-11 ***					0.163739	0.000251 ***	3.49e-11 ***	0.006834 **		3.51e-06 ***
MOD_172	2.00e-05 ***	8.38e-05 ***	4.06e-12 ***		3.55e-16 ***	6.92e-08 ***					0.61332	0.000774 ***	1.81e-12 ***			
MOD_173	0.002293 **	0.000102 ***	8.56e-14 ***	6.06e-07 ***	5.00e-10 ***		0.002504 **						1.83e-12 ***			

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
MOD_174	0.025902 *	4.11e-06 ***	8.92e-12 ***	1.14e-07 ***	< 2e-16 ***	0.000241 ***	3.39e-09 ***	4.70e-08 ***			0.001013 **		1.01e-10 ***		1.06e-08 ***	1.74e-09 ***
MOD_175	0.000758 ***	3.30e-05 ***	2.57e-12 ***		< 2e-16 ***	1.12e-07 ***	0.000211 ***				0.112705	2.40e-05 ***	4.36e-12 ***			4.59e-07 ***
MOD_176	0.00122 **	1.16e-06 ***	1.55e-12 ***		2.49e-12 ***	1.44e-07 ***	0.00311 **			0.13624		2.50e-08 ***	2.19e-14 ***			1.01e-06 ***
MOD_177	2.02e-05 ***	2.98e-05 ***	3.78e-12 ***		< 2e-16 ***	6.56e-08 ***			0.963			1.85e-08 ***	2.42e-12 ***			
MOD_178	0.000754 ***	3.44e-06 ***	1.06e-11 ***		3.82e-15 ***	8.83e-11 ***			0.437705			1.41e-07 ***	7.66e-13 ***	0.028319 *		6.73e-06 ***
MOD_179	0.000799 ***	9.27e-06 ***	1.20e-11 ***	7.20e-14 ***	3.45e-15 ***	1.81e-15 ***	0.335658									
MOD_180	0.00182 **	5.05e-07 ***	1.13e-12 ***		3.51e-11 ***	3.74e-08 ***	0.00264 **	0.00503 **				1.70e-09 ***	1.70e-13 ***	0.02612 *		1.71e-05 ***
MOD_181	0.000516 ***	7.13e-07 ***	2.76e-12 ***		< 2e-16 ***	3.43e-07 ***	0.001419 **		0.563683			2.01e-09 ***	1.52e-13 ***			1.29e-06 ***
MOD_182	0.000206 ***	3.28e-06 ***	3.80e-12 ***		8.04e-13 ***	0.003226 **	1.52e-05 ***	0.003884 **				2.74e-08 ***	2.32e-14 ***		0.001824 **	2.77e-05 ***
MOD_183	0.00365 **	1.84e-06 ***	1.82e-12 ***	2.84e-10 ***	2.35e-13 ***	0.00411 **	1.57e-05 ***		0.5896				1.21e-09 ***	0.00654 **	4.04e-07 ***	0.00197 **
MOD_184	0.000299 ***	1.86e-05 ***	9.13e-11 ***	0.11856	< 2e-16 ***	2.90e-10 ***		0.003919 **				1.59e-08 ***	1.34e-10 ***			2.89e-05 ***
MOD_185	0.006390 **	5.56e-06 ***	2.40e-11 ***	0.022568 *	8.69e-13 ***	1.09e-11 ***		0.000429 ***				2.97e-08 ***	7.37e-11 ***	0.001270 **		4.77e-06 ***
MOD_186	0.000522 ***	4.49e-06 ***	2.33e-11 ***	1.04e-08 ***	< 2e-16 ***	1.52e-06 ***			0.966924				9.45e-09 ***	0.004010 **	0.000336 ***	0.005724 **
MOD_187	0.00036 ***	8.40e-06 ***	2.38e-11 ***		5.14e-11 ***	6.36e-07 ***		0.00302 **				1.12e-06 ***	6.36e-13 ***	0.00327 **	0.02929 *	4.51e-05 ***
MOD_188	5.91e-05 ***	1.52e-05 ***	2.21e-13 ***		4.18e-12 ***	1.40e-06 ***							1.43e-10 ***	0.0104 *		
MOD_189	0.0424 *	6.65e-05 ***	3.61e-14 ***	2.66e-06 ***								9.68e-10 ***	5.71e-15 ***			
MOD_190	0.004680 **	4.63e-06 ***	3.69e-12 ***	0.010517 *	< 2e-16 ***	4.39e-09 ***	4.82e-05 ***	0.000376 ***				2.07e-10 ***	2.48e-11 ***			2.31e-06 ***
MOD_191	0.003061 **	0.000584 ***	7.03e-11 ***	1.76e-13 ***	< 2e-16 ***	< 2e-16 ***	0.007167 **					0.003648 **				4.31e-06 ***
MOD_192	0.001546 **	7.59e-06 ***	1.70e-12 ***		3.73e-09 ***	0.001879 **	9.30e-05 ***	0.002097 **				2.48e-07 ***	5.13e-14 ***	0.024748 *	0.000947 ***	2.56e-05 ***
MOD_193	0.000781	0.000149	1.53e-11		4.98e-12	1.97e-11		0.004657			0.136458	8.58e-05	5.81e-11	0.002070		1.69e-05

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
	***	***	***		***	***		**				***	***	**		***
MOD_194	5.62e-07 ***	1.56e-05 ***	5.92e-10 ***	0.0133 *	6.66e-15 ***	0.0270 *							3.27e-09 ***			
MOD_195	0.000842 ***	2.12e-06 ***	1.29e-12 ***		2.38e-10 ***	2.88e-08 ***	0.002876 **	0.005105 **		0.066464 .		3.49e-09 ***	5.57e-14 ***			1.31e-05 ***
MOD_196	0.000584 ***	5.77e-06 ***	1.14e-11 ***		8.55e-13 ***	2.69e-11 ***		0.005160 **	0.404275			1.75e-08 ***	1.43e-12 ***	0.012258 *		2.21e-05 ***
MOD_197	2.30e-05 ***	4.45e-05 ***	3.64e-13 ***		1.18e-11 ***								9.90e-15 ***			
MOD_198	0.000554 ***	0.000119 ***	3.46e-12 ***		6.15e-15 ***	0.000797 ***	1.48e-05 ***				0.139607	0.000118 ***	1.12e-12 ***		0.006391 **	6.13e-06 ***
MOD_199	0.030609 *	2.75e-07 ***	1.54e-12 ***	0.002562 **	2.75e-13 ***	4.07e-10 ***	0.000314 ***	7.81e-05 ***				1.09e-09 ***	2.21e-11 ***	0.006518 **		7.35e-07 ***
MOD_200	0.000817 ***	4.95e-06 ***	2.40e-12 ***		3.44e-11 ***	0.001010 **	0.000227 ***			0.180896		8.88e-07 ***	7.52e-15 ***		0.006162 **	1.38e-05 ***
MOD_201	0.000373 ***	9.55e-05 ***	2.17e-12 ***		3.49e-15 ***	3.41e-08 ***	0.000103 ***	0.007905 **			0.094247 .	7.25e-06 ***	9.19e-12 ***			1.52e-05 ***
MOD_202	0.004439 **	4.84e-06 ***	8.91e-11 ***	2.01e-05 ***	8.12e-12 ***	1.18e-07 ***		3.56e-06 ***					2.84e-08 ***	0.000101 ***	4.37e-07 ***	9.03e-08 ***
MOD_203	8.69e-06 ***	2.95e-06 ***	8.65e-12 ***	0.865	< 2e-16 ***	1.02e-07 ***							5.55e-10 ***			9.95e-07 ***
MOD_204	0.000383 ***	5.95e-06 ***	3.70e-12 ***		4.59e-15 ***	0.002982 **	8.37e-05 ***		0.970446			1.56e-07 ***	6.71e-14 ***		0.005758 **	3.10e-05 ***
MOD_205	0.000278 ***	3.03e-06 ***	2.75e-12 ***		< 2e-16 ***	1.02e-07 ***	0.000922 ***	0.008137 **	0.472428			2.28e-10 ***	2.94e-13 ***			1.89e-05 ***
MOD_206	2.03e-05 ***	1.35e-05 ***	1.98e-13 ***		1.52e-10 ***	6.42e-07 ***				0.0107 *			5.51e-11 ***			
MOD_207	4.95e-05 ***	6.93e-05 ***	4.63e-11 ***	0.401028	< 2e-16 ***	7.75e-09 ***					0.31201	0.000375 ***	1.99e-11 ***			1.35e-05 ***
MOD_208	3.27e-06 ***	3.64e-06 ***	1.57e-12 ***		< 2e-16 ***	7.67e-07 ***		0.0167 *					1.26e-10 ***			
MOD_209	0.002833 **	8.30e-05 ***	7.58e-13 ***		1.71e-10 ***	4.18e-09 ***	0.000493 ***	0.003879 **			0.038574 *	3.66e-06 ***	1.95e-11 ***	0.010519 *		1.08e-05 ***
MOD_210	1.47e-05 ***	0.000182 ***	1.31e-11 ***	0.007421 **	4.53e-11 ***							3.17e-07 ***	< 2e-16 ***			0.004032 **
MOD_211	0.000216 ***	2.40e-05 ***	5.89e-11 ***	0.097648 .	< 2e-16 ***	6.17e-10 ***		0.003147 **			0.000236 ***		1.09e-10 ***			2.40e-05 ***
MOD_212	0.003049 **	2.52e-05 ***	2.05e-12 ***	0.012204 *	< 2e-16 ***	4.17e-09 ***	4.08e-05 ***	0.000341 ***			5.45e-07 ***		2.70e-11 ***			2.33e-06 ***

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
MOD_213	0.003925 **	2.39e-05 ***	1.85e-11 ***	0.026992 *	2.48e-13 ***	1.87e-11 ***		0.000475 ***			6.12e-05 ***		1.03e-10 ***	0.001743 **		5.18e-06 ***
MOD_214	0.000721 ***	5.42e-05 ***	1.33e-11 ***	0.425468	1.05e-13 ***	1.00e-09 ***					0.143077	0.000180 ***	3.19e-11 ***	0.007650 **		1.46e-05 ***
MOD_215	0.000548 ***	8.17e-06 ***	2.23e-12 ***		6.18e-09 ***	0.001043 **	0.000145 ***	0.002556 **		0.094975 .		2.40e-07 ***	2.12e-14 ***		0.002593 **	2.05e-05 ***
MOD_216	1.07e-05 ***	8.35e-06 ***	2.04e-13 ***		1.07e-15 ***	0.000142 ***	0.138446						2.04e-10 ***			
MOD_217	0.000264 ***	6.69e-05 ***	3.23e-12 ***		9.05e-13 ***	0.001093 **	4.93e-06 ***	0.003980 **			0.130177	5.44e-05 ***	2.19e-12 ***		0.002791 **	2.11e-05 ***
MOD_218	0.000656 ***	3.85e-05 ***	2.48e-12 ***	0.64467	< 2e-16 ***	3.80e-07 ***	0.000279 ***				0.103965	2.09e-05 ***	5.33e-12 ***			1.13e-06 ***
MOD_219	0.00175 **	1.57e-06 ***	1.21e-12 ***		2.82e-11 ***	3.49e-08 ***	0.00347 **	0.00501 **	0.66294			1.63e-09 ***	3.97e-13 ***	0.03915 *		1.90e-05 ***
MOD_220	3.56e-06 ***	9.31e-06 ***	8.23e-13 ***		< 2e-16 ***	4.37e-06 ***			0.396				7.84e-09 ***			
MOD_221	0.018949 *	2.63e-05 ***	8.57e-13 ***	0.003944 **	7.67e-12 ***	3.10e-10 ***	0.000182 ***	8.51e-05 ***			1.99e-07 ***		3.84e-11 ***	0.006992 **		8.59e-07 ***
MOD_222	0.0432 *	1.00e-05 ***	< 2e-16 ***				5.63e-08 ***					5.27e-10 ***	< 2e-16 ***			
MOD_223	0.000207 ***	3.31e-06 ***	3.95e-12 ***		7.34e-13 ***	0.004139 **	3.48e-05 ***	0.928977				3.23e-08 ***	1.46e-13 ***		0.002421 **	3.54e-05 ***
MOD_224	0.002402 **	5.29e-05 ***	1.13e-12 ***		2.78e-10 ***	0.000314 ***	1.99e-05 ***	0.001865 **			0.052707 .	3.11e-05 ***	5.07e-12 ***	0.011269 *	0.001646 **	1.58e-05 ***
MOD_225	0.00047 ***	7.10e-05 ***	2.72e-11 ***		9.09e-11 ***	3.24e-07 ***		0.00301 **			0.20017	0.00055 ***	2.97e-11 ***	0.00176 **	0.05293 .	3.36e-05 ***
MOD_226	0.000365 ***	8.28e-06 ***	2.26e-11 ***		3.55e-11 ***	4.91e-07 ***		0.003069 **	0.540489			9.50e-07 ***	1.19e-12 ***	0.007447 **	0.035055 *	4.64e-05 ***
MOD_227	0.002312 **	2.03e-05 ***	1.55e-11 ***	0.029295 *	9.14e-12 ***	2.28e-11 ***		0.000528 ***		0.005601 **	0.000520 ***		1.29e-10 ***			4.60e-06 ***
MOD_228	0.000279 ***	5.15e-05 ***	1.57e-11 ***	0.412255	1.14e-12 ***	1.09e-09 ***				0.027920 *	0.23232	0.000353 ***	1.51e-11 ***			8.30e-06 ***
MOD_229	0.001550 **	7.58e-06 ***	1.74e-12 ***		4.75e-09 ***	0.002654 **	0.000118 ***	0.002120 **	0.890616			3.39e-07 ***	1.84e-13 ***	0.027083 *	0.001040 **	3.76e-05 ***
MOD_230	7.91e-06 ***	1.52e-06 ***	2.34e-12 ***	0.096205 .	2.84e-13 ***								3.37e-15 ***			0.000333 ***
MOD_231	0.016987 *	0.000169 ***	7.47e-15 ***									3.63e-08 ***	1.58e-15 ***			
MOD_232	0.0658 .	5.95e-05	< 2e-16	1.05e-06			1.07e-05						7.42e-11			

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
		***	***	***			***						***			
MOD_233	0.00629 **	2.22e-05 ***	4.21e-15 ***										1.02e-13 ***	1.12e-05 ***		
MOD_234	0.02774 *	0.00013 ***	9.38e-15 ***	8.10e-06 ***									6.02e-10 ***			
MOD_235	0.00331 **	2.69e-05 ***	2.26e-15 ***							7.69e-06 ***			1.81e-14 ***			
MOD_236	8.82e-06 ***	5.21e-07 ***	2.24e-10 ***		< 2e-16 ***	< 2e-16 ***										3.77e-06 ***
MOD_237	4.46e-06 ***	5.73e-05 ***	2.89e-11 ***		< 2e-16 ***	< 2e-16 ***										
MOD_238	0.014125 *	0.000148 ***	6.84e-15 ***								8.82e-07 ***		8.00e-14 ***			
MOD_239	0.0039 **	1.30e-06 ***	1.83e-14 ***										6.21e-12 ***		1.61e-05 ***	
MOD_240	0.00989 **	6.98e-06 ***	< 2e-16 ***				1.32e-05 ***						1.00e-12 ***			
MOD_241	0.036547 *	0.000102 ***	8.84e-15 ***	3.79e-06 ***		0.283784							1.66e-07 ***			
MOD_242	0.00544 **	6.07e-08 ***	2.64e-15 ***										8.71e-12 ***			
MOD_243	0.027091 *	0.000121 ***	1.78e-14 ***	2.08e-05 ***									7.24e-10 ***			0.517517
MOD_244	1.01e-05 ***	3.14e-05 ***	3.69e-11 ***		4.63e-16 ***	1.12e-15 ***						0.000922 ***				
MOD_245	0.000335 ***	4.64e-06 ***	1.20e-11 ***		9.24e-14 ***	0.004349 **							1.02e-09 ***			
MOD_246	0.025 *	7.76e-05 ***	1.75e-13 ***	1.72e-10 ***		2.50e-08 ***										
MOD_247	5.21e-06 ***	5.57e-05 ***	3.04e-11 ***		1.65e-15 ***	< 2e-16 ***	0.816									
MOD_248	0.000624 ***	0.000107 ***	9.87e-11 ***	3.02e-12 ***	3.93e-07 ***											
MOD_249	0.0520 .	5.32e-05 ***	7.52e-14 ***	1.99e-11 ***		3.39e-08 ***	0.0345 *									
MOD_250	9.43e-08 ***	2.24e-06 ***	.59e-08 ***		7.83e-13 ***											
MOD_251	0.00726 **	2.15e-05 ***	2.21e-14 ***										3.05e-11 ***			0.01718 *

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
MOD_252	0.00602 **	9.36e-05 ***	4.85e-11 ***	4.20e-13 ***	3.84e-06 ***		0.01349 *									
MOD_253	0.00111 **	5.58e-06 ***	2.87e-13 ***										3.16e-10 ***			
MOD_254	0.000645 ***	2.87e-05 ***	1.30e-10 ***	0.661307	2.63e-13 ***	0.000681 ***						6.93e-07 ***	3.07e-11 ***			
MOD_255	0.001774 **	0.000421 ***	8.93e-11 ***	8.05e-10 ***	5.51e-07 ***							5.95e-05 ***				
MOD_256	0.001774 **	0.000364 ***	8.93e-11 ***	8.05e-10 ***	5.51e-07 ***							5.95e-05 ***				
MOD_257	0.0067 **	2.70e-05 ***	5.11e-15 ***					0.6297					1.09e-11 ***			
MOD_258	0.00509 **	2.25e-05 ***	2.26e-15 ***						0.46506				2.68e-10 ***			
MOD_259	0.0056 **	2.04e-05 ***	3.26e-15 ***			0.635							4.63e-10 ***			
MOD_260	0.050790 .	0.000361 ***	5.07e-13 ***	1.66e-10 ***		7.35e-08 ***						0.015059 *				
MOD_261	0.000431 ***	4.82e-06 ***	1.63e-11 ***	0.779133	8.25e-14 ***	0.006217 **							1.80e-08 ***			
MOD_262	0.0277 *	3.36e-05 ***	3.47e-13 ***	5.89e-10 ***		4.55e-08 ***										0.2324
MOD_263	0.000497 ***	9.00e-05 ***	1.96e-10 ***	1.73e-11 ***	2.50e-07 ***											0.182299
MOD_264	0.004228 **	0.000153 ***	4.28e-12 ***	3.48e-10 ***												
MOD_265	0.018381 *	0.000125 ***	1.72e-12 ***	6.63e-11 ***			0.008442 **									
MOD_266	0.053647 .	0.000759 ***	5.86e-13 ***	4.78e-09 ***			0.011196 *					1.01e-05 ***				
MOD_267	0.018561 *	0.000845 ***	3.98e-12 ***	3.25e-08 ***								6.42e-05 ***				
MOD_268	0.0293 *	4.14e-07 ***	7.16e-14 ***										2.92e-10 ***			
MOD_269	0.004003 **	0.000134 ***	8.50e-12 ***	1.90e-09 ***												0.262752
MOD_270	0.00169 **	3.03e-06 ***	2.80e-13 ***			6.63e-12 ***										
MOD_271	2.36e-05	2.78e-06	4.69e-12		1.90e-07						1.36e-07					

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
	***	***	***		***						***					
MOD_272	6.25e-05 ***	0.000253 ***	3.00e-11 ***		2.43e-06 ***							8.40e-08 ***				
MOD_273	2.42e-05 ***	4.39e-05 ***	9.23e-11 ***		4.35e-07 ***				5.86e-06 ***							
MOD_274	0.00354 **	2.86e-06 ***	1.70e-13 ***			2.91e-10 ***	0.09522 .									
MOD_275	0.00337 **	6.74e-06 ***	1.89e-12 ***			3.31e-11 ***										0.00257 **
MOD_276	7.78e-06 ***	3.34e-06 ***	4.09e-10 ***		1.35e-07 ***										3.34e-06 ***	
MOD_277	0.004978 **	0.000263 ***	2.37e-13 ***			6.86e-07 ***						0.000998 ***				
MOD_278	0.000213 ***	0.000261 ***	4.93e-12 ***		7.20e-05 ***		0.004108 **					1.07e-08 ***				
MOD_279	1.58e-05 ***	2.50e-05 ***	1.03e-10 ***		4.11e-05 ***											
MOD_280	1.76e-05 ***	0.000349 ***	1.65e-10 ***													
MOD_281	0.002226 **	0.000334 ***	1.23e-12 ***									4.71e-07 ***				
MOD_282	0.005538 **	0.000286 ***	1.73e-13 ***				0.006555 **					4.23e-08 ***				
MOD_283	0.000952 ***	1.46e-05 ***	1.76e-13 ***								1.07e-05 ***					
MOD_284	1.87e-05 ***	2.27e-05 ***	5.60e-10 ***		2.07e-05 ***											2.07e-05 ***
MOD_285	1.87e-05 ***	2.27e-05 ***	5.60e-10 ***		2.07e-05 ***											0.000571 ***
MOD_286	0.000200 ***	3.27e-06 ***	1.74e-11 ***												1.86e-05 ***	
MOD_287	0.000142 *	2.62e-05 ***	5.71e-11 ***		0.000515		0.029260 *									
MOD_288	0.000142 ***	2.62e-05 ***	5.71e-11 ***		0.000515 ***		0.029260 *									
MOD_289	0.000626 ***	3.04e-05 ***	2.07e-12 ***						0.000128 ***							
MOD_290	0.003102 **	0.000355 ***	1.21e-11 ***									1.30e-06 ***				0.001747 **

Model ID	Covariate															
	Width field	Speed	Douglas	SST	CHL	ZEU	ZEU_STD	PAR	PAR_STD	DEP	DEP_ASP_sin	DEP_ASP_cos	DEP_SL	Depth	YEAR	MONTH
MOD_291	0.000885 ***	1.90e-05 ***	2.66e-12 ***				0.006498 **									
MOD_292	0.000187 ***	2.67e-05 ***	2.49e-10 ***		4.12e-05 ***											
MOD_293	0.000284 ***	1.75e-05 ***	3.56e-11 ***													0.000682 ***
MOD_294	9.42e-06 ***	8.91e-06 ***	1.31e-10 ***		9.19e-06 ***					0.102						
MOD_295	3.77e-05 ***	9.16e-06 ***	1.76e-10 ***		5.79e-05 ***			0.152								
MOD_296	0.00166 **	1.60e-05 ***	1.64e-11 ***													
MOD_297	0.000320 ***	2.61e-05 ***	1.02e-11 ***					0.110075								
MOD_298	0.000146 ***	1.80e-05 ***	8.65e-12 ***							0.344863						
MOD_299	0.008364 **	0.000280 ***	5.92e-14 ***			1.21e-06 ***	0.026893 *					0.000213 ***				
MOD_300	0.008830 **	0.000228 ***	1.23e-12 ***				0.000105 ***					3.65e-08 ***				0.000139 ***
MOD_301	0.103	1.97e-06 ***	2.36e-16 ***	3.12e-07 ***			3.75e-08 ***					8.80e-12 ***	< 2e-16 ***			
MOD_302	0.000402 ***	5.15e-05 ***	6.71e-14 ***				9.89e-06 ***					5.83e-09 ***	< 2e-16 ***			
MOD_303	0.0454 *	2.95e-08 ***	< 2e-16 ***			0.8037	2.91e-07 ***					5.03e-10 ***	1.11e-15 ***			
MOD_304	0.08966 .	4.94e-06 ***	4.11e-16 ***				3.53e-09 ***					4.57e-10 ***	< 2e-16 ***			0.00161 **
MOD_305	0.002405 **	0.000202 ***	2.47e-13 ***	1.65e-08 ***	2.59e-09 ***		7.07e-06 ***					3.37e-11 ***	< 2e-16 ***			
MOD_306	0.000112 ***	9.45e-06 ***	3.28e-13 ***		1.88e-13 ***	1.51e-05 ***	0.003655 **					7.78e-10 ***	1.26e-14 ***			
MOD_307	0.00105 **	2.33e-05 ***	4.40e-13 ***		1.10e-09 ***		4.07e-07 ***					1.88e-08 ***	< 2e-16 ***			3.46e-05 ***

Appendix IX. Observation points along the Galician coast a) kept for the whole study period and, b) dropped out according with Pierce et al 2010. The alphanumeric code is the identification code of the Observation Point at the database of CEMMA.

Observation Point				Latitude	Longitude
1	SA.1	LU1-I-B	Pta. do Castro, Reinante	43.563	-7.177
2		LU1-I-C	Pto. de Burela	43.656	-7.344
3	SA.2	C2-II-C	Estaca de Bares	43.786	-7.677
4		C2-II-D	Mdor. Sto. Antonio, Espasante	43.726	-7.810
5		C2-III-A	F. Cabo Ortegal	43.771	-7.870
6		C2-III-C	F. Pta. Candieira	43.710	-8.048
7		C2-III-E	F. Cabo Prior	43.568	-8.314
8		C3-IV-A	A Graña/ Cabo Prioriño	43.470 / 43.460	-8.269 / -8.340
9	SA.3	C3-V-A	Pta. Alta. Barrañán	43.313	-8.561
10		C3-V-B	Pta. das Olas, Caión	43.322	-8.607
11		C3-V-D	C. San Adrián	43.340	-8.831
12		C3-VI-A	F. O Roncudo, Corme	43.275	-8.991
13		C3-VI-C	F. Cabo Vilán	43.159	-9.211
14		C3-VI-D	C. Touriñán	43.055	-9.298
15	SA.4	C4-VII-A	C. Fisterra	42.882	-9.272
16		C4-VII-C	Pta. Remedios, Lira	42.802	-9.150
17		C4-VII-E	Tal, vértice xeodésico	42.780	-9.002
18		C4-VIII-B	Castro de Baroña	42.695	-9.033
19		C4-VIII-C	F. Corrubedo	42.576	-9.090
20	SA.5	C5-IX-C	Pta. Cabío	42.587	-8.921
21		PO5-X-E	Pto. de Tragove	42.518	-8.829
22		PO5-X-C	Mdor. de Raeiros	42.458	-8.889
23		PO5-X-B	Mdor. de Barreiros	42.398	-8.793
24		PO5-XI-A	Mdor. de Mogor	42.387	-8.719
25	SA.6	PO6-XII-D	Monte Facho	42.271	-8.862
26		PO6-XII-C	Pta. Balea	42.248	-8.788
27		PO6-XII-B	Pto. de O Con	42.271	-8.737
28		PO6-XIII-B	F. Silleiro	42.105	-8.896
29		PO6-XIII-C	Mdor. de Oia	41.988	-8.884
30		PO6-XIII-D	Mdor. de A Guarda	41,914	-8,885

Appendix IX. Continued.

b)

Observation Point			Latitude	Longitude
SA. 1	LU1-I-A	F. Illa Pancha	43.555	-7.043
	LU1-I-D	F. San Cibrán	43.700	-7.436
	LU1-II-A	F. Pta. Roncadoira	43.736	-7.525
	LU1-II-B	Pta. do Faro	43.712	-7.583
SA. 2	C2-III-B	Cruceiro de Teixidelo	43.711	-7.975
	C2-III-D	Pta. Corveira	43.643	-8.123
SA. 3	C3-IV-B	Pto. de Sada	43.363	-8.244
	C3-IV-B	Faros de Mera	43.363	-8.244
	C3-IV-D	Monte San Pedro	43.376	-8.394
	C3-V-C	P. Baldaio	43.304	-8.655
	C3-VI-B	Laxe	43.232	-9.011
SA. 4	C4-VII-B	F. de Cee	42.916	-9.184
	C4-VII-D	F. Monte Louro	42.739	-9.079
	C4-VIII-A	Virxe de Loreto	42.743	-8.984
	C5-IX-A	P. Vilar	42.552	-9.028
SA. 5	C5-IX-B	Pto. de Riveira	42.560	-8.987
	C5-IX-D	Cabo de Cruz	42.611	-8.887
	PO5-X-D	Pta. Pateiro	42.476	-8.939
	PO5-X-A	Pto. de Combarro	42.427	-8.705
	PO5-XI-B	Pto. de Bueu	42.329	-8.788
	PO5-XI-BB	Burato do Inferno	42.361	-8.947
	PO5-XI-C	C. Udra	42.334	-8.833
SA. 6	PO6-XII-A	S. Adrián de Cobres	42.302	-8.655
	PO6-XIII-A	A Bombardeira	42.122	-8.859

Appendix X. Hours of observation at 30 Observation Points along the Galician coast a) per year and b) per month.

a)

	Sub-area	SA.1		SA.2						SA.3						SA.4				
Observation Point		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Year	2003	0.52	-	1.88	1.33	1.37	0.67	0.75	0.87	1.20	1.57	1.67	1.50	1.83	2.38	2.62	2.50	0.37	2.00	2.17
	2004	5.50	5.27	11.38	6.17	6.62	7.67	6.63	4.05	5.17	5.83	6.75	5.62	5.52	5.55	9.18	6.58	7.07	9.07	6.90
	2005	5.20	5.67	6.67	6.37	6.37	5.53	5.33	5.17	7.77	7.30	7.20	5.82	5.35	6.05	7.35	6.23	6.98	8.08	7.00
	2006	1.00	5.08	7.75	4.95	7.05	3.50	7.00	3.67	12.48	6.40	9.13	7.63	7.22	7.67	10.37	7.50	7.93	9.98	7.63
	2007	7.80	10.68	7.10	6.82	7.92	6.08	11.08	0.33	8.32	5.28	8.25	5.62	6.15	5.83	11.62	6.38	6.60	11.78	18.75
	2008	10.35	8.13	9.38	9.07	9.07	8.87	7.70	0.00	7.52	7.50	7.62	6.40	6.50	6.50	8.17	7.67	6.98	9.98	8.67
	2009	8.20	8.08	8.08	8.28	8.33	8.07	7.97	4.23	10.08	8.25	7.68	6.67	6.67	6.67	7.50	7.05	7.12	7.03	8.08
	2010	6.67	6.83	7.85	6.50	8.48	6.67	7.50	6.67	7.08	7.72	5.08	6.33	6.75	6.17	7.00	4.67	5.75	8.67	5.83
	2011	5.23	6.05	6.22	5.67	6.37	5.87	5.90	5.78	6.98	6.50	5.52	4.50	4.83	5.72	6.63	4.50	7.00	6.77	6.77

	Sub-area	SA.5					SA.6						
Observation Point		20	21	22	23	24	25	26	27	28	29	30	TOTAL
Year	2003	3.05	3.42	5.62	6.83	2.53	4.58	4.00	7.27	6.50	2.78	3.17	77.27
	2004	6.82	13.55	15.80	30.32	7.12	10.72	12.08	14.67	12.52	7.60	6.80	269.17
	2005	7.00	8.07	8.52	14.78	6.10	6.18	7.17	5.88	6.37	5.62	5.22	208.57
	2006	7.95	6.03	7.72	10.43	8.23	5.92	6.88	6.88	8.95	5.83	5.42	219.55
	2007	11.73	5.83	5.93	10.58	8.57	6.67	7.20	5.88	10.08	6.35	6.33	242.10
	2008	8.67	8.33	7.33	8.75	8.83	7.00	7.00	7.50	7.50	7.17	6.87	237.22
	2009	8.33	8.08	8.25	8.50	7.83	7.25	7.33	7.33	7.00	7.03	6.75	235.78
	2010	5.50	8.08	7.30	7.17	7.00	7.67	8.00	8.00	6.83	6.67	7.17	212.27
	2011	6.58	6.08	6.50	5.58	6.67	6.25	6.50	5.67	7.83	8.00	7.58	189.05

Appendix X. Continued.

b)

	Sub-area	SA.1		SA.2						SA.3						SA.4				
	Observation Point	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
Month	Jan	3.50	3.33	2.45	4.33	5.58	4.75	4.92	2.98	4.42	4.00	4.15	3.05	2.70	2.55	4.72	4.18	4.25	5.67	5.33
	Feb	3.92	5.53	19.07	2.62	4.78	4.33	8.50	1.50	3.65	3.17	4.03	3.90	3.53	4.25	5.42	3.25	3.67	4.10	4.20
	Mar	4.28	3.67	6.42	4.63	5.42	4.92	5.00	2.17	5..03	5.12	5.48	3.65	3.28	2.72	5.78	3.68	3.72	5.75	5.18
	Apr	4.12	5.10	12.58	4.75	5.37	4.37	4.72	1.58	4.25	4.53	4.87	4.73	4.55	4.75	6.20	4.37	4.60	5.83	7.08
	May	3.57	4.08	20.97	4.25	4.58	3.92	4.47	1.97	5.13	4.82	4.42	3.53	3.78	4.33	5.67	5.15	4.92	4.20	6.22
	Jun	3.67	3.83	3.50	3.68	4.42	3.50	4.17	2.12	4.97	4.80	4.53	3.85	3.67	3.67	5.25	4.87	3.92	4.78	6.00
	Jul	4.47	4.88	1.33	4.80	4.53	4.03	4.08	2.50	8.88	5.57	4.83	4.58	5.00	5.42	5.17	3.83	4.92	8.53	8.07
	Aug	5.22	4.95	0.00	4.75	5.20	4.63	4.75	3.05	8.58	4.43	5.67	5.48	5.35	5.47	7.75	5.62	7.83	6.50	6.68
	Sep	4.10	5.12	0.00	5.40	4.67	4.78	4.92	3.28	5.80	5.10	5.62	4.20	4.42	4.30	5.15	3.45	4.00	5.47	7.03
	Oct	5.32	5.23	0.00	5.17	5.00	4.47	5.28	3.58	5.33	4.87	6.05	4.50	4.17	4.75	6.83	5.00	5.25	7.28	5.75
	Nov	4.08	5.28	0.00	5.17	5.42	4.47	4.27	2.83	5.08	4.63	3.63	4.17	5.20	4.83	6.83	4.97	4.65	5.75	3.00
	Dec	4.23	4.78	0.00	5.60	6.60	4.75	4.80	3.20	5.47	5.32	5.62	4.43	5.17	5.50	5.67	4.72	4.08	7.50	7.25

Appendix X. Continued.

b)

	Sub-area	SA.5					SA.6						
Observation Point		**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**TOTAL**
Month	Jan	6.68	5.72	5.05	7.10	5.00	2.58	2.03	2.25	6.20	4.10	3.53	131.75
	Feb	4.50	5.52	7.70	8.17	5.03	4.98	4.75	5.08	6.42	5.42	5.25	144.42
	Mar	6.10	5.73	7.32	7.03	5.88	6.88	7.87	9.00	8.33	5.35	5.25	138.73
	Apr	5.00	4.97	4.60	7.42	5.47	4.92	5.25	4.83	5.37	4.50	4.47	147.80
	May	4.37	5.12	5.90	6.25	5.33	3.82	6.37	4.58	6.12	5.33	4.42	163.15
	Jun	5.45	4.90	5.43	11.23	4.00	4.87	5.13	4.58	4.67	4.20	4.17	157.52
	Jul	4.20	5.35	5.15	10.77	4.37	6.68	7.10	7.07	4.90	4.23	3.75	156.78
	Aug	5.73	6.30	5.38	7.58	5.38	4.92	5.00	4.88	5.67	5.00	4.83	167.10
	Sep	6.10	7.83	7.83	13.63	6.38	7.58	7.17	10.35	7.38	5.00	5.25	190.50
	Oct	5.20	6.25	6.33	7.92	5.30	5.55	5.92	7.10	5.92	3.92	4.30	179.93
	Nov	4.73	4.82	5.60	6.07	4.98	5.78	5.75	5.77	4.92	3.83	3.83	152.23
	Dec	7.57	4.98	6.67	9.78	5.75	3.67	3.83	3.58	7.70	6.17	6.25	159.05

Appendix XI. Models for the study of the covariates affecting the observer with their values of Deviation Explained (Dev. Expl.) and AIC. Covariates: height of the observation station in meters (Height_m), number of observers (N_Obs), optics used by the observers (Optics_N), Beaufort, North component of the wind (W_north), Wester component of the wind (W_East), Douglas, Visibility, Area expressed in Km^2 (Area_Km2), minutes of duration of the observation (Obs_min), presence of bottlenose dolphins (Sight_TTR).

Model ID	Model	Dev. Expl.	AIC
MOD_01	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3)	11.6%	743.06
MOD_02	Y ~ 1 + s(Obs_min k = 3) + s(AKm2, k=3) + s(Beaufort, k=3) + s(Sight_TTR, k=3)	11.00%	744.77
MOD_03	Y ~ 1 + s(Obs_min k = 3) + s(AKm2, k=3) + s(Beaufort, k=3) + s(Douglas, k=3)	10.60%	749.11
MOD_04	Y ~ 1 + s(Obs_min k = 3) + s(AKm2, k=3) + s(Beaufort, k=3) + s(Opt_n, k=3)	10.20%	750.31
MOD_05	Y ~ 1 + s(Obs_min, k = 3) + s(AKm2, k=3) + s(Beaufort, k=3)	9.78%	752.45
MOD_06	Y ~ 1 + s(Obs_min k = 3) + s(AKm2, k=3) + s(Beaufort, k=3) + s(Visib, k=3)	9.89%	753.56
MOD_07	Y ~ 1 + s(Obs_min k = 3) + s(AKm2, k=3) + s(Beaufort, k=3) + s(Height_TTR, k=3)	9.79%	754.25
MOD_08	Y ~ 1 + s(Obs_min k = 3) + s(AKm2, k=3) + s(Beaufort, k=3) + s(N_Obs, k=3)	9.79%	754.35
MOD_09	Y ~ 1 + s(Obs_min, k = 3) + s(AKm2, k=3) + s(Sight_TTR, k=3)	9.19%	757.69
MOD_10	Y ~ 1 + s(Obs_min, k = 3) + s(AKm2, k=3) + s(Optics, k=3)	8.57%	761.92
MOD_11	Y ~ 1 + s(Obs_min k = 3) + s(AreaKm2, k=3)	8.17%	764.03
MOD_12	Y~ 1 + s(Obs_min, k = 3) + s(AKm2, k=3) + s(Visib, k=3)	8.32%	764.86
MOD_13	Y ~ 1 + s(Obs_min, k = 3) + s(AKm2, k=3) + s(Douglas, k=3)	8.45%	764.9
MOD_14	Y ~ 1 + s(Obs_min, k = 3) + s(AKm2, k=3) + s(N_Obs)	8.21%	765.71
MOD_15	Y ~ 1 + s(Obs_min, k = 3) + s(AKm2, k=3) + s(Hm, k=3)	8.16%	765.98
MOD_16	Y ~ 1 + s(Obs_min k = 3) + s(Beaufort, k=3)	7.21%	770.05
MOD_17	Y ~ 1 + s(Obs_min k = 3) + s(Optics_n, k=3)	6.00%	779.6
MOD_18	Y ~ 1 + s(Obs_min k = 3) + s(Sight_TTR, k=3)	5.68%	782.92
MOD_19	Y ~ 1 + s(Obs_min k = 3)	4.94%	787.03

Model ID	Model	Dev. Expl.	AIC
MOD_20	Y ~ 1 + s(Obs_min k = 3) + s(Douglas, k=3)	4.99%	788.58
MOD_21	Y ~ 1 + s(Obs_min k = 3) + s(Hm, k=3)	4.96%	788.69
MOD_22	Y ~ 1 + s(Obs_min k = 3) + s(N_Obs, k=3)	4.94%	789.01
MOD_23	Y ~ 1 + s(Obs_min k = 3) + s(Visib, k=3)	4.94%	789.01
MOD_24	Y ~ 1 + s(Area_Km2, k = 3)	3.13%	800.17
MOD_25	Y ~ 1 + s(Beaufort, k = 3)	2.62%	804.04
MOD_26	Y ~ 1 + s(Optics_N, k = 3)	1.12%	815.91
MOD_27	Y ~ 1 + s(Sight_TTR k = 3)	0.27%	823.69
MOD_28	Y ~ 1 + s(Douglas, k = 3)	0.08%	825.18
MOD_29	Y ~ 1 + s(Visibility, k = 3)	0.09%	825.2
MOD_30	Y ~ 1 + s(Height_m, k = 3)	0.03%	825.53
MOD_31	Y ~ 1 + s(N_Obs, k = 3)	0.03%	825.7

Appendix XII. P-values of the models for the study of the covariates affecting the observer. Covariates: height of the observation station in meters (Height_m), number of observers (N_Obs), optics used by the observers (Optics_N), Beaufort, North component of the wind (W_north), Wester component of the wind (W_East), Douglas, Visibility, Area expressed in Km^2 (Area_Km2), minutes of duration of the observation (Obs_min), presence of bottlenose dolphins (Sight_TTR).

Model ID	Covariate										
	Height_m	N_Obs	Optics_N	Beaufort	W_north	W_East	Douglas	Visibility	Area_Km2	Obs_min	Sight_TTR
MOD_01				< 2e-16 ***			0.000271 ***		< 2e-16 ***	< 2e-16 ***	3.21e-08 ***
MOD_02				< 2e-16 ***					< 2e-16 ***	< 2e-16 ***	2.98e-09 ***
MOD_03				< 2e-16 ***			1.05e-05 ***		< 2e-16 ***	< 2e-16 ***	
MOD_04			2.57e-05 ***	1.46e-15 ***					< 2e-16 ***	< 2e-16 ***	
MOD_05				1.92e-15 ***					< 2e-16 ***	< 2e-16 ***	
MOD_06				3.29e-15 ***				0.0371 *	< 2e-16 ***	< 2e-16 ***	
MOD_07	0.378			1.43e-15 ***					< 2e-16 ***	< 2e-16 ***	
MOD_08		0.49		3.24e-15 ***					< 2e-16 ***	< 2e-16 ***	
MOD_09									< 2e-16 ***	< 2e-16 ***	3.51e-08 ***
MOD_10			3.93e-05 ***						< 2e-16 ***	< 2e-16 ***	
MOD_11									<2e-16 ***	<2e-16 ***	
MOD_12								0.0173 *	<2e-16 ***	<2e-16 ***	
MOD_13							0.0823		<2e-16 ***	<2e-16 ***	
MOD_14		0.22							<2e-16 ***	<2e-16 ***	
MOD_15	0.974								<2e-16 ***	<2e-16 ***	
MOD_16				<2e-16						<2e-16	

Model ID	Covariate										
	Height_m	N_Obs	Optics_N	Beaufort	W_north	W_East	Douglas	Visibility	Area_Km2	Obs_min	Sight_TTR
				***						***	
MOD_17			9e-09 ***							<2e-16 ***	
MOD_18										< 2e-16 ***	1.80e-06 ***
MOD_19										<2e-16 ***	
MOD_20							0.146			<2e-16 ***	
MOD_21	0.265									<2e-16 ***	
MOD_22		0.737								<2e-16 ***	
MOD_23								0.73		<2e-16 ***	
MOD_24									<2e-16 ***		
MOD_25				<2e-16 ***							
MOD_26			1.27e-08 ***								
MOD_27											0.0034 **
MOD_28							0.0747				
MOD_29								0.0695			
MOD_30	0.261										
MOD_31		0.305									

Appendix XIII. Models for the study of the covariates affecting the observer plus spatiotemporal covariates with their values of Deviation Explained (Dev. Expl.) and AIC. Covariates: station of observation (PC), day of the year (Day_of_Year), year as smoother, year as factor (as.facto(Year), time of the day when the observation starts (START_OBS), Beaufort, Douglas, area surveyed by observers in Km^2 (Area_Km2), minutes of observation (Obs_min), presence of bottlenose dolphins (Sight_TTR).

Model ID	Model	Dev. Expl.	AIC
MOD_01	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(YEAR, k = 4) + s(START_OBS, k = 4) + s(PC)	17.2%	709.11
MOD_02	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(PC) + s(YEAR, k = 4) + s(START_OBS, k = 4)	17.3%	710.12
MOD_03	Y ~ 1 + as.factor(YEAR) + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(PC) + s(START_OBS, k = 4) + s(Day_of_Year)	19.2%	710.9
MOD_04	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(YEAR, k = 4) + s(START_OBS, k = 4) + s(Day_of_Year) + s(PC)	17.3%	712.06
MOD_05	Y ~ 1 + as.factor(YEAR) + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(PC)	18.5%	712.79
MOD_06	Y ~ 1 + as.factor(YEAR) + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(PC)	18.5%	712.79
MOD_07	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(PC) + (YEAR, k = 4)	16.6%	714.05
MOD_08	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(YEAR, k = 4) + s(Day_of_Year) + s(PC)	16.7%	715.69
MOD_09	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(PC) + s(START_OBS, k = 4)	16.2%	717.34
MOD_10	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(PC) + s(Day_of_Year)	15.8%	721.57
MOD_11	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(YEAR, k = 4) + s(START_OBS, k = 4)	13.2%	733.72
MOD_12	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(YEAR, k = 4) + s(START_OBS, k = 4) + s(Day_of_Year)	13.3%	735.42
MOD_13	Y ~ 1 + as.factor(YEAR) + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3)	14.3%	736.85
MOD_14	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(YEAR, k = 4) + s(Day_of_Year)	12.7%	739.36
MOD_15	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(START_OBS, k = 4)	12.2%	739.62
MOD_16	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(START_OBS, k = 4) + s(Day_of_Year)	12.4%	741.12
MOD_17	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(Day_of_Year)	11.9%	743.89

Appendix XIV. P-values of the models for the study of the covariates affecting the observer plus spatiotemporal covariates. P-values: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. Covariates: station of observation (PC), day of the year (Day_of_Year), year as smoother, year as factor (as.facto(Year), time of the day when the observation starts (START_OBS), Beaufort, Douglas, area surveyed by observers in Km^2 (Area_Km2), minutes of observation (Obs_min), presence of bottlenose dolphins (Sight_TTR).

Model ID	Covariates									
	PC	Day_of_Year	Year	as.factor (Year)	START_OBS	Beaufort	Douglas	Area_Km2	Obs_min	Sight_TTR
MOD_01	< 2e-16 ***		1.40e-11 ***		9.16e-09 ***	< 2e-16 ***		< 2e-16 ***	< 2e-16 ***	2.43e-07 ***
MOD_02	< 2e-16 ***		1.41e-12 ***		2.12e-08 ***	< 2e-16 ***	0.0289 *	< 2e-16 ***	< 2e-16 ***	1.93e-07 ***
MOD_03	< 2e-16 ***	0.4259		1	2.26e-08 ***	< 2e-16 ***	0.0745 .	5.75e-12 ***	< 2e-16 ***	3.87e-08 ***
MOD_04	< 2e-16 ***	0.5900	1.53e-12 ***		2.55e-08 ***	< 2e-16 ***	0.0344 *	< 2e-16 ***	< 2e-16 ***	1.97e-07 ***
MOD_05	< 2e-16 ***					< 2e-16 ***	0.0302 *	3.55e-11 ***	< 2e-16 ***	4.13e-08 ***
MOD_06	< 2e-16 ***			1		< 2e-16 ***	0.0302 *	3.55e-11 ***	< 2e-16 ***	4.13e-08 ***
MOD_07	< 2e-16 ***		2.36e-11 ***			< 2e-16 ***	0.0118 *	4.76e-15 ***	< 2e-16 ***	2.04e-07 ***
MOD_08	< 2e-16 ***	0.2512	3.66e-11 ***			< 2e-16 ***	0.0283 *	3.96e-15 ***	< 2e-16 ***	1.68e-07 ***
MOD_09	< 2e-16 ***				3.63e-07 ***	< 2e-16 ***	0.94	< 2e-16 ***	< 2e-16 ***	7.48e-07 ***
MOD_10	< 2e-16 ***	0.0899 .				< 2e-16 ***	0.9670	< 2e-16 ***	< 2e-16 ***	6.4e-07 ***
MOD_11			1.00e-10 ***		1.21e-08 ***	< 2e-16 ***	0.00758 **	< 2e-16 ***	< 2e-16 ***	6.25e-09 ***
MOD_12		0.21153	1.29e-10 ***		2.46e-08 ***	< 2e-16 ***	0.00732 **	< 2e-16 ***	< 2e-16 ***	7.48e-09 ***
MOD_13				1		< 2e-16 ***	0.0149 *	< 2e-16 ***	< 2e-16 ***	4.76e-10 ***
MOD_14		0.04797 *	2.77e-09 ***			< 2e-16 ***	0.00698 **	< 2e-16 ***	< 2e-16 ***	4.91e-09 ***
MOD_15					1.97e-07 ***	< 2e-16 ***	0.000196 ***	< 2e-16 ***	< 2e-16 ***	5.09e-08 ***
MOD_16		0.122			5.51e-07 ***	< 2e-16 ***	8.92e-05 ***	< 2e-16 ***	< 2e-16 ***	6.04e-08 ***
MOD_17		0.0197 *				< 2e-16 ***	7.38e-05 ***	< 2e-16 ***	< 2e-16 ***	3.76e-08 ***

Appendix XV. Models for the study of the covariates affecting the observer plus environmental covariates with their values of Deviation Explained (Dev. Expl.) and AIC.

Model_ID	Model	Dev. Expl.	AIC
MOD_001	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(D_200m, k=4)	22.70%	541.092
MOD_002	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(POP_STD, k =4)+ s(ASP_cos, k =4)	23.70%	541.183
MOD_003	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(POP_STD, k =4)	22.90%	541.228
MOD_004	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ZEU_MEAN, K=4) + s(ASP_scos, K=4)	23.30%	541.49
MOD_005	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ZEU_MEAN, K=4) + s(ASP_STD, K=4)	22.90%	541.511
MOD_006	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(POP_STD, k =4)+ s(ASP_STD, k =4)	23.20%	541.623
MOD_007	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ZEU_MEAN, K=4) + s(Start_Obs, K=4)	22.80%	541.943
MOD_008	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ZEU_MEAN, K=4) + s(SST_STD, K=4)	22.80%	542.086
MOD_009	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(POP_STD, k =4)+ s(Start_Obs, k =4)	23.10%	542.104
MOD_010	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(POP_STD, k =4)+ s(SST_STD, k =4)	23.10%	542.265
MOD_011	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)	22.10%	542.669
MOD_012	Y3 ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ZEU_MEAN, K=4) + s(ZEU_STD, K=4)	22.70%	542.809
MOD_013	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(POP_STD, k =4)+ s(ZEU_STD, k =4)	23.00%	542.846
MOD_014	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ZEU_MEAN, K=4) + s(PAR_STD, K=4)	22.70%	542.927
MOD_015	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ZEU_MEAN, K=4) + s(SST_MEAN, K=4)	22.70%	542.965
MOD_016	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ZEU_MEAN, K=4) + s(CHL_MEAN, K=4)	22.70%	543.014
MOD_017	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ASP_sin, K=4)	22.40%	543.027
MOD_018	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+	22.70%	543.028

Model_ID	Model	Dev. Expl.	AIC
	s(ZEU_MEAN, K=4) + s(ASP_sin, K=4)		
MOD_019	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ZEU_MEAN, K=4) + s(PAR_MEAN, K=4)	22.70%	543.054
MOD_020	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(POP_STD, k =4)+ s(PAR_STD, k =4)	23.00%	543.069
MOD_021	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ZEU_MEAN, K=4) + s(CHL_STD, K=4)	22.70%	543.078
MOD_022	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(POP_STD, k =4)+ s(SST_MEAN, k =4)	23.00%	543.117
MOD_023	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(POP_STD, k =4)+ s(PAR_MEAN, k =4)	23.00%	543.119
MOD_024	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(POP_STD, k =4)+ s(CHL_MEAN, k =4)	23.00%	543.155
MOD_025	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(POP_STD, k =4)+ s(POP_sin, k =4)	23.00%	543.172
MOD_026	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(POP_STD, k =4)+ s(CHL_STD, k =4)	23.00%	543.197
MOD_027	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(Start_Obs, K=4)	22.30%	543.218
MOD_028	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ASP_cos, K=4)	22.70%	543.264
MOD_029	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ZEU_STD, K=4)	22.30%	543.274
MOD_030	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(SST_STD, K=4)	22.20%	543.867
MOD_031	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(SST_MEAN, K=4)	22.20%	544.034
MOD_032	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(CHL_MEAN, K=4)	22.20%	544.039
MOD_033	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(PAR_STD, K=4)	22.20%	544.288
MOD_034	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(CHL_STD, K=4)	22.20%	544.334
MOD_035	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(PAR_MEAN, K=4)	22.10%	544.556
MOD_036	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SLO_MEAN, K=4)+ s(ASP_STD, K=4)	22.10%	544.636
MOD_037	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(ASP_cos, k =4)	22.80%	545.341
MOD_038	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(ASP_cos, K=4)	22.10%	545.391

Model_ID	Model	Dev. Expl.	AIC
MOD_039	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(ZEU_MEAN, K=4)	21.70%	545.733
MOD_040	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4)	21.30%	546.229
MOD_041	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4)	21.50%	546.393
MOD_042	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4)	21.80%	546.501
MOD_043	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(ASP_STD, k=4)	21.80%	546.776
MOD_044	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(Start_obs, K=4)	21.50%	546.776
MOD_045	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(ZEU_STD, K=4)	21.50%	547.145
MOD_046	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(ASP_cos, k=4)	22.10%	547.433
MOD_047	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(Start_Obs, k=4)	21.70%	547.464
MOD_048	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(CHL_MEAN, K=4)	21.40%	547.597
MOD_049	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(SST_STD, k=4)	21.70%	547.633
MOD_050	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SST_MEAN, K=4)	21.40%	547.694
MOD_051	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(CHL_STD, K=4)	21.30%	547.879
MOD_052	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(SST_STD, K=4)	21.30%	547.922
MOD_053	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(ASP_STD, K=4)	21.40%	547.977
MOD_054	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(DEP_STD, k=4)	22.00%	548.023
MOD_055	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(ZEU_STD, k=4)	21.60%	548.075
MOD_056	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(PAR_MEAN, K=4)	21.30%	548.081
MOD_057	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(PAR_STD, k=4)	21.60%	548.118
MOD_058	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(PAR_STD, K=4)	21.30%	548.177
MOD_059	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(SST_MEAN, k=4)	21.60%	548.18
MOD_060	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Dist_200m, K=4) + s(ASP_sin, K=4)	21.30%	548.223

Model_ID	Model	Dev. Expl.	AIC
MOD_061	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(ASP_sin, k=4)	21.60%	548.322
MOD_062	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(PAR_MEAN, k=4)	21.60%	548.323
MOD_063	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(CHL_MEAN, k=4)	21.60%	548.357
MOD_064	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) +s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(POP_STD, k=4) + s(CHL_STD, k=4)	21.50%	548.392
MOD_065	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(ASP_ASP, k =4)	22.30%	548.417
MOD_066	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4)	21.50%	548.601
MOD_067	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_cos, k =4)	21.70%	548.852
MOD_068	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(DEP_STD, k=4)	21.60%	548.903
MOD_069	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(SST_STD, k =4)	21.60%	549.608
MOD_070	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(Start_obs, k =4)	21.60%	549.874
MOD_071	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(ASP_sin, k =4)	21.60%	550.013
MOD_072	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(PAR_STD, k =4)	21.60%	550.047
MOD_073	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_cos, k =4) + s(ZEU_STD, k =4)	21.80%	550.155
MOD_074	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_cos, k =4) + s(POP_STD, k =4)	21.80%	550.159
MOD_075	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(ZEU_STD, k =4)	21.60%	550.177
MOD_076	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_cos, k =4) + s(SST_STD, k =4)	21.80%	550.223
MOD_077	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_cos, k =4) + s(ASP_STD, k =4)	21.70%	550.326
MOD_078	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(PAR_MEAN, k =4)	21.60%	550.355
MOD_079	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_cos, k =4) + s(Start_Obs, k =4)	21.80%	550.446
MOD_080	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(CHL_MEAN, k =4)	21.50%	550.46
MOD_081	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) +	21.50%	550.476

Model_ID	Model	Dev. Expl.	AIC
	s(DEP_STD, k =4) + s(SST_MEAN, k =4)		
MOD_082	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_cos, k =4) + s(PAR_MEAN, k =4)	21.90%	550.492
MOD_083	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(DEP_STD, k =4) + s(CHL_MEAN, k =4)	21.50%	550.571
MOD_084	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(ASP_cos, k=4)	21.80%	550.601
MOD_085	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_cos, k =4) + s(PAR_STD, k =4)	21.80%	550.602
MOD_086	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_cos, k =4) + s(SST_MEAN, k =4)	21.70%	550.659
MOD_087	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_cos, k =4) + s(CHL_MEAN, k =4)	21.70%	550.729
MOD_088	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_cos, k =4) + s(ASP_sin, k =4)	21.70%	550.74
MOD_089	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(POP_STD, k =4)	20.90%	550.799
MOD_090	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_cos, k =4) + s(CHL_STD, k =4)	21.70%	550.814
MOD_091	Y A~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4)	20.50%	550.929
MOD_092	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_STD, k =4)	21.00%	551.93
MOD_093	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(ASP_sin, k=4)	21.20%	552.12
MOD_094	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(SST.STD, k =4)	20.70%	552.132
MOD_095	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(ZEU_STD, k=4)	21.20%	552.205
MOD_096	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4)	20.60%	552.255
MOD_097	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(DEP_STD, k=4)	20.30%	552.344
MOD_098	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(ZEU_MEAN, K=4)	20.40%	552.372
MOD_099	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(Start_Obs, k =4)	20.60%	552.376
MOD_100	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(DEP_STD, k=4)	20.60%	552.462
MOD_101	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ZEU_STD, k =4)	20.60%	552.517

Model_ID	Model	Dev. Expl.	AIC
MOD_102	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4)	22.70%	552.542
MOD_103	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(PAR_MEAN, k =4)	23.70%	552.617
MOD_104	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(SST.MEAN, k =4)	20.30%	552.671
MOD_105	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4)	20.70%	552.681
MOD_106	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(ASP_STD, k=4)	20.60%	552.753
MOD_107	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(PAR_STD, k =4)	20.80%	552.767
MOD_108	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(CHL.MEAN, k =4)	21.30%	552.833
MOD_109	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(ASP_sin, k =4)	20.60%	552.839
MOD_110	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(D_200, k=4) + s(CHL.STD, k =4)	20.60%	552.904
MOD_111	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(POP_STD, k=4)	20.50%	553.043
MOD_112	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(POP_STD, k=4)	20.50%	553.226
MOD_113	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(POP_STD, k=4) + s(ZEU_STDN, k=4)	20.20%	553.305
MOD_114	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(Start_Obs, K=4)	21.00%	553.321
MOD_115	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(ZEU_STD, K=4)	20.50%	553.477
MOD_116	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(POP_STD, k=4) + s(ASP_sin, k=4)	20.20%	553.513
MOD_117	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(ASP_cos, K=4)	20.20%	553.616
MOD_118	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(CHL_MEAN, k=4)	20.40%	553.655
MOD_119	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(SST_MEAN, k=4)	20.10%	553.69
MOD_120	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(DEP_STD, k=4)	21.00%	553.7015
MOD_121	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(CHL_MEAN, K=4)	21.00%	553.769
MOD_122	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(SST_MEAN, K=4)	20.70%	553.865
MOD_123	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN,	20.10%	553.907

Model_ID	Model	Dev. Expl.	AIC
	k=4) + s(DEP_STD, k=4)		
MOD_124	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4)	20.10%	553.985
MOD_125	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(ASP_STD, K=4)	20.70%	553.991
MOD_126	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(POP_STD, k=4) + s(SST_MEAN, k=4)	20.90%	553.992
MOD_127	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(Start_Obs, k=4)	20.20%	554.012
MOD_128	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(CHL_STD, K=4)	20.40%	554.023
MOD_129	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(PAR_STD, k=4)	20.90%	554.088
MOD_130	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(POP_STD, k=4) + s(Start_Obs, k=4)	20.10%	554.117
MOD_131	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(PAR_MEAN, K=4)	20.90%	554.19
MOD_132	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(SST_STD, k=4)	20.40%	554.219
MOD_133	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(ASP_STD, k=4)	20.10%	554.222
MOD_134	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(PAR_MEAN, k=4)	20.60%	554.224
MOD_135	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(CHL_STD, k=4)	21.00%	554.236
MOD_136	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_cos, k=4) + s(SST_STD, k=4)	20.90%	554.258
MOD_137	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(PAR_STD, k=4)	20.90%	554.297
MOD_138	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(SST_STD, K=4)	20.90%	554.307
MOD_139	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4)	20.60%	554.328
MOD_140	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(POP_STD, k=4) + s(CHL_MEAN, k=4)	20.00%	554.361
MOD_141	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(ASP_sin, k=4)	20.00%	554.367
MOD_142	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(PAR_STD, K=4)	20.30%	554.394
MOD_143	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(Start_Obs, k=4)	20.60%	554.406
MOD_144	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4)	20.00%	554.416

Model_ID	Model	Dev. Expl.	AIC
MOD_145	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(POP_STD, K=4) + s(ASP_sin, K=4)	20.60%	554.478
MOD_146	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(ZEU_STD, k=4)	20.30%	554.493
MOD_147	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(POP_STD, k=4) + s(SST_STD, k=4)	20.00%	554.581
MOD_148	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(POP_STD, k=4) + s(PAR_MEAN, k=4)	20.60%	554.637
MOD_149	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(PAR_MEAN, k=4)	20.30%	554.723
MOD_150	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(SST_MEAN, k=4)	20.30%	554.745
MOD_151	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(POP_STD, k=4) + s(CHL_STD, k=4)	20.60%	554.747
MOD_152	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(POP_STD, k=4)	20.50%	554.757
MOD_153	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(POP_STD, k=4) + s(ASP_STD, k=4)	20.30%	554.869
MOD_154	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(CHL_MEAN, k=4)	20.30%	554.892
MOD_155	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(ASP_cos, k=4)	20.30%	554.892
MOD_156	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(POP_STD, k=4) + s(PAR_STD, k=4)	20.50%	554.898
MOD_157	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(DEP_STD, k=4) + s(CHL_STD, k=4)	20.80%	554.966
MOD_158	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_sin, k=4)	20.20%	555.403
MOD_159	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(Dist_200m, K=4)	20.50%	555.533
MOD_160	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4)	20.10%	556.268
MOD_161	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(POP_STD, k=4)	20.10%	556.438
MOD_162	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ZEU_STD, k=4)	19.70%	556.604
MOD_163	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(CHL_MEAN, k=4)	20.00%	556.791
MOD_164	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4)	20.00%	556.798
MOD_165	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(ASPSTD, k=4)	20.00%	556.958

Model_ID	Model	Dev. Expl.	AIC
MOD_166	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(DEP_STD, k=4)	19.60%	557.448
MOD_167	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(SST_STD, k=4)	20.10%	557.773
MOD_168	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(ZEU_STD, k=4)	19.80%	557.888
MOD_169	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(SST_MEAN, k=4)	19.80%	557.889
MOD_170	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(Start_Obs, k=4)	19.80%	557.947
MOD_171	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(Start_Obs, k=4)	19.80%	557.953
MOD_172	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(CHL_STD, k=4)	19.80%	557.958
MOD_173	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(PAR_MEAN, k=4)	19.80%	558.063
MOD_174	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(SST_MEAN, k=4)	19.80%	558.076
MOD_175	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(ASP_sin, k=4)	19.80%	558.1
MOD_176	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(PAR_STD, k=4)	19.80%	558.157
MOD_177	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(CHL_STD, k=4)	19.70%	558.259
MOD_178	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_MEAN, k=4) + s(CHL_MEAN, k=4)	19.70%	558.265
MOD_179	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(ASP_cos, K=4)	19.70%	558.28
MOD_180	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ASP_cos, k=4)	19.70%	558.317
MOD_181	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(SST_STD, k=4)	20.20%	558.342
MOD_182	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(PAR_STD, k=4)	19.90%	558.459
MOD_183	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(PAR_MEAN, k=4)	19.70%	558.478
MOD_184	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(ZEU_MEAN, K=4)	19.70%	558.483
MOD_185	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(D_200m, k=4) + s(ASP_STD, k=4)	19.70%	558.622
MOD_186	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(POP_STD, k=4)	19.70%	558.818

Model_ID	Model	Dev. Expl.	AIC
MOD_187	Y~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ASP_sin, k=4)	19.80%	559.125
MOD_188	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(ASP_STD, K=4)	19.30%	560.191
MOD_189	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ZEU_STD, k=4)	19.30%	560.23
MOD_190	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(CHL_MEAN, k=4)	19.00%	560.299
MOD_191	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(ASP_STD, K=4)	19.10%	560.353
MOD_192	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4)	19.20%	560.355
MOD_193	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4)	19.30%	560.516
MOD_194	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(ZEU_STD, K=4)	18.80%	560.926
MOD_195	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(CHL_MEAN, K=4)	19.10%	561.125
MOD_196	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(SST_MEAN, k=4)	19.30%	561.313
MOD_197	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(CHL_STD, k=4)	19.30%	561.391
MOD_198	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(CHL_STD, K=4)	19.00%	561.655
MOD_199	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(ASP_sin, K=4)	18.90%	561.676
MOD_200	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(ASP_STD, K=4)	19.20%	561.692
MOD_201	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(Start_Obs, K=4)	19.20%	561.718
MOD_202	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(Start_Obs, k=4)	19.10%	561.745
MOD_203	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(PAR_MEAN, k=4)	19.20%	561.893
MOD_204	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(ASP_STD, K=4)	18.90%	561.921
MOD_205	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(PAR_STD, k=4)	18.90%	561.961
MOD_206	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(SST_MEAN, K=4)	19.30%	561.965
MOD_207	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(SST_STD, k=4)	18.90%	562.042
MOD_208	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SLO_MEAN, K=4) + s(ASP_STD, k=4)	19.20%	562.144
MOD_209	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(PAR_STD, K=4)	18.80%	562.211
MOD_210	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(PAR_MEAN, K=4)	18.90%	562.23

Model_ID	Model	Dev. Expl.	AIC
MOD_211	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(DEP_STD, K=4) + s(SST_STD, K=4)	19.10%	562.442
MOD_212	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(asp_STD, K=4)	19.10%	580.028
MOD_213	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(ZEU_MEAN, K=4)	19.10%	582.745
MOD_214	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(pop_STD, K=4)	16.20%	584.316
MOD_215	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(Dist_200, K=4)	15.40%	587.562
MOD_216	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(CHL_MEAN, K=4)	15.70%	587.793
MOD_217	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(ZEU_STD, K=4)	14.80%	589.859
MOD_218	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4)	14.60%	590.977
MOD_219	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(CHL_STD, K=4)	14.30%	591.119
MOD_220	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(Asp_COS, K=4)	13.90%	591.268
MOD_221	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(Start_Obs, K=4)	14.10%	591.622
MOD_222	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SST_MEAN, K=4)	14.10%	591.709
MOD_223	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(PAR_MEAN, K=4)	14.10%	591.918
MOD_224	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(ASP_sin, K=4)	14.00%	592.288
MOD_225	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(SST_STD, K=4)	14.00%	592.29
MOD_226	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(W_Northing, k = 4) + s(PAR_STD, K=4)	14.10%	592.298
MOD_227	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(W_Northing, k = 4)	14.00%	594.492
MOD_228	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(POP_STD, K=4)	14.10%	683.777
MOD_229	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(DIST_200m, K=4)	12.80%	683.888
MOD_230	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(Start_Obs, K=4)	19.60%	684.95
MOD_231	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(PAR_STD, K=4)	19.60%	685.386
MOD_232	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(ZEU_MEAN, K=4)	19.50%	686.007
MOD_233	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(ASP_STD, K=4)	19.70%	686.434
MOD_234	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(SLO_MEAN, K=4)	19.30%	686.719

Model_ID	Model	Dev. Expl.	AIC
MOD_235	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4)	19.40%	686.72
MOD_236	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(CHL_MEAN, K=4)	19.00%	686.933
MOD_237	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DEP_STD, k = 4)	19.00%	687.375
MOD_238	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(ASP_cos, K=4)	19.20%	687.669
MOD_239	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(ZEU_STD, K=4)	18.70%	687.907
MOD_240	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(PAR_MEAN, K=4)	19.50%	687.983
MOD_241	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(CHL_STD, K=4)	19.10%	688.027
MOD_242	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(SST_MEAN, K=4)	19.10%	688.237
MOD_243	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(ASP_sin, K=4)	19.10%	688.531
MOD_244	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DEP_STD, k = 4) + s(SST_STD, K=4)	19.00%	688.562
MOD_245	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(SLO_MEAN, k = 4)	19.00%	694.323
MOD_246	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(SLO_MEAN, k = 4)	19.00%	694.574
MOD_247	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(ASP_STD, k = 4)	17.50%	717.863
MOD_248	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(ASP_STD, k = 4)	17.70%	719.866
MOD_249	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(POP_STD, k = 4)	14.80%	731.567
MOD_250	Y~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(ZEU_MEAN, k = 4)	14.80%	732.017
MOD_251	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(POP_STD, k = 4)	13.30%	732.788
MOD_252	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(ZEU_MEAN, k = 4)	12.90%	733.06
MOD_253	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3)+ s(CHL_MEAN, k = 4)	13.50%	735.438
MOD_254	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(PAR_STD, k = 4)	13.10%	735.793
MOD_255	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(PAR_STD, k = 4)	12.30%	736.045
MOD_256	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(CHL_MEAN, k = 4)	12.70%	736.281
MOD_257	Y~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(ASP_COS, k = 4)	13.00%	738.585
MOD_258	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(ASP_COS, k = 4)	12.60%	739.256

Model_ID	Model	Dev. Expl.	AIC
MOD_259	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(START_OBS, k = 4)	12.00%	739.617
MOD_260	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(ASP_SIN, k = 4)	12.30%	740.113
MOD_261	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(ASP_SIN, k = 4)	12.20%	740.935
MOD_262	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(START_OBS, k = 4)	12.10%	741.401
MOD_263	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(ZEU_STD, k = 4)	12.30%	741.779
MOD_264	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(DIST_200, k = 4)	11.60%	741.954
MOD_265	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(PAR_MEAN, k = 4)	12.00%	742.77
MOD_266	Y~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) +s(ZEU_STD, k = 4)	12.00%	742.799
MOD_267	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(CHL_STD, k = 4)	11.90%	742.829
MOD_268	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(CHL_STD, k = 4)	11.40%	743.35
MOD_269	Y~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DIST_200, k = 4)	11.80%	743.594
MOD_270	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(SST_MEAN, k = 4)	11.40%	743.733
MOD_271	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(DOUGLAS, k = 3) + s(SST_STD, 4)	11.40%	743.886
MOD_272	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(SST_STD, 4)	11.70%	744.558
MOD_273	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(PAR_MEAN, k = 4)	11.70%	745.144
MOD_274	Y ~ 1 + s(OBS_min, k = 3) + s(AREA_km2, k = 3) + s(BEAUFORT, k = 3) + s(Sighting_TTR, k = 3) + s(SST_MEAN, k = 4)	11.20%	745.956

Appendix XVI. P-values of the models for the study of the covariates affecting the observer plus environmental covariates. P-values: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. Covariates: minutes of observation (Obs_min), area surveyed by observers in Km^2 (Area_Km2), Beaufort, presence of bottlenose dolphins (Sight_TTR), Douglas, sea surface temperature (SST), chlorophyll concentration (CHL), euphotic depth (ZEU), photosynthetically active radiation (PAR), depth (DEP), seabed slope (SLO), seabed aspect (ASP_sin, ASP_cos), and their standard deviations (SST-STD, CHL-STD, ZEU-STD, PAR-STD, DEP-STD, SLO-STD, ASP-STD), standar desviation of the human population (POP_STD), distance from the OP to the 200m isobaths (Dist_200m), Northing component of the wind (W_north).

Model_ID	Covariates																				
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_001	4.63e-06 ***	0.000870 ***	0.000218 ***							0.066090 .				0.021609 *	0.012757 *				0.005106 **	0.009024 **	0.046065 *	
MOD_002	1.52e-06 ***	0.000883 ***	0.000883 ***	0.164714						0.054429 .				0.023487 *	0.030881 *		0.137651		0.017177 *	0.007172 **	0.045971 *	
MOD_003	2.12e-06 ***	0.000716 ***	0.000215 ***	0.194147						0.066302 .				0.025780 *	0.013772 *				0.005254 **	0.009198 **	0.048966 *	
MOD_004	3.74e-06 ***	0.001096 **	0.000149 ***							0.059117 .				0.017541 *	0.037047 *		0.177287		0.013751 *	0.007002 **	0.044283 *	
MOD_005	6.36e-06 ***	0.001269 **	0.000211 ***							0.023074 *				0.027819 *	0.015665 *			0.192513	0.005674 **	0.009265 **	0.052005 .	
MOD_006	3.03e-06 ***	0.001046 **	0.000202 ***	0.190672						0.015820 *				0.024959 *	0.022817 *			0.190708	0.005434 **	0.009180 **	0.054751 .	
MOD_007	2.52e-06 ***	0.000755 ***	0.000211 ***							0.079155 .				0.021426 *	0.014339 *				0.004313 **	0.008059 **	0.044951 *	0.314201
MOD_008	4.1e-06 ***	0.001152 **	0.000231 ***				0.306522			0.058009 .				0.022070 *	0.009585 **				0.005215 **	0.007951 **	0.048989 *	
MOD_009	1.16e-06 ***	0.000626 ***	0.000207 ***	0.196782						0.078820 .				0.022813 *	0.013677 *				0.004416 **	0.008072 **	0.048320 *	0.320950
MOD_010	1.92e-06 ***	0.000944 ***	0.000231 ***	0.199213			0.318916			0.058276 .				0.021697 *	0.009205 **				0.005361 **	0.008047 **	0.051999 .	
MOD_011	1.4e-05 ***	0.000557 ***	0.000189 ***											0.025297 *	0.021296 *				0.002132 **	0.010662 *	0.080955 .	
MOD_012	3.96e-06 ***	0.000845 ***	0.000223 ***							0.129799	0.612760			0.023419 *	0.012664 *				0.005205 **	0.009184 **	0.044929 *	
MOD_013	1.76e-06 ***	0.000689 ***	0.000220 ***	0.185309						0.137274	0.555628			0.025359 *	0.012386 *				0.005357 **	0.009312 **	0.046892 *	
MOD_014	5.5e-06 ***	0.000812 ***	0.000224 ***							0.075078 .			0.727958	0.021383 *	0.012187 *				0.005961 **	0.009470 **	0.045084 *	
MOD_015	5.6e-06 ***	0.000903 ***	0.000254 ***			0.694198				0.095170 .				0.026027 *	0.013140 *				0.005105 **	0.009456 **	0.049765 *	
MOD_016	4.5e-06 ***	0.000852 ***	0.000227 ***					0.750830		0.085392 .				0.026485 *	0.012971 *				0.005260 **	0.008811 **	0.047329 *	
MOD_017	8.63e-06 ***	0.000946 ***	0.000191 ***											0.022809 *	0.010553 *	0.223496			0.005145 **	0.009986 **	0.062511 .	

Model_ID	Covariates																				
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_018	4.97e-06 ***	0.000890 ***	0.000217 ***							0.174600				0.023612 *	0.021801 *	0.827261			0.006004 **	0.009045 **	0.045603 *	
MOD_019	4.96e-06 ***	0.000901 ***	0.000225 ***							0.069390 .		0.905591		0.022335 *	0.013032 *				0.005227 **	0.009174 **	0.048097 *	
MOD_020	2.53e-06 ***	0.000671 ***	0.000221 ***	0.194727						0.075150 .			0.734267	0.025449 *	0.012190 *				0.006084 **	0.009615 **	0.047907 *	
MOD_021	4.56e-06 ***	0.000879 ***	0.000220 ***						0.917335	0.079599 .				0.024231 *	0.013331 *				0.005119 **	0.009023 **	0.046166 *	
MOD_022	2.58e-06 ***	0.000732 ***	0.000250 ***	0.196349		0.717005				0.093872 .				0.028140 *	0.012598 *				0.005273 **	0.009621 **	0.052608 .	
MOD_023	2.21e-06 ***	0.000751 ***	0.000226 ***	0.189091						0.068494 .		0.850499		0.026855 *	0.012538 *				0.005441 **	0.009385 **	0.052019 .	
MOD_024	2.06e-06 ***	0.000702 ***	0.000224 ***	0.194803				0.759695		0.086951 .				0.029708 *	0.013113 *				0.005406 **	0.008938 **	0.050119 .	
MOD_025	2.24e-06 ***	0.000741 ***	0.000214 ***	0.194853						0.170902				0.009203 **	0.022567 *	0.842974			0.006233 **	0.023189 *	0.048420 *	
MOD_026	2.07e-06 ***	0.000717 ***	0.000217 ***	0.192738					0.875744	0.076560 .				0.026632 *	0.013060 *				0.005253 **	0.009034 **	0.048963 *	
MOD_027	6.74e-06 ***	0.000474 ***	0.000189 ***											0.022788 *	0.022002 *				0.001876 **	0.009232 **	0.076334 .	0.257383
MOD_028	9.37e-06 ***	0.001554 **	0.000139 ***											0.018090 *	0.057512 .		0.453770		0.007915 **	0.008794 **	0.089509 .	
MOD_029	7.82e-06 ***	0.000476 ***	0.000212 ***								0.257240			0.026495 *	0.018444 *				0.002623 **	0.010518 *	0.067565 .	
MOD_030	1.29e-05 ***	0.000706 ***	0.000204 ***				0.361402							0.026518 *	0.017038 *				0.002109 **	0.009645 **	0.085498 .	
MOD_031	1.55e-05 ***	0.000559 ***	0.000257 ***			0.422073								0.028071 *	0.020697 *				0.002295 **	0.011348 *	0.085378 .	
MOD_032	1.17e-05 ***	0.000565 ***	0.000180 ***					0.495060						0.025203 *	0.022328 *				0.002445 **	0.010900 *	0.069505 .	
MOD_033	1.67e-05 ***	0.000505 ***	0.000199 ***										0.577983	0.024457 *	0.018464 *				0.002784 **	0.011350 *	0.077520 .	
MOD_034	1.36e-05 ***	0.000583 ***	0.000182 ***						0.598533					0.027156 *	0.021657 *				0.002307 **	0.011122 *	0.075456 .	
MOD_035	1.55e-05 ***	0.000555 ***	0.000194 ***									0.737439		0.026938 *	0.022082 *				0.002260 **	0.011468 *	0.084193 .	
MOD_036	1.42e-05 ***	0.001533 **	0.000187 ***											0.025925 *	0.023715 *			0.779746	0.002195 **	0.010774 *	0.087946 .	
MOD_037	3.84e-06 ***	0.000583 ***	0.000181 ***	0.137015						0.028216 *				0.149650	0.020350 *		0.035802 *			0.009527 **	0.045495 *	
MOD_038	7.14e-06 ***	0.002021 **	0.000128 ***											0.005517 **			0.192412		0.005555 **	0.005050 **	0.064144 .	
MOD_039	6.77e-06 ***	0.001316 **	0.000185 ***							0.129616				0.025254 *					0.011257 *	0.004673 **	0.027445 *	
MOD_040	1.28e-05 ***	0.001759 **	0.000176 ***											0.022790 *					0.004765 **	0.010701 *	0.056126 .	

Model_ID	Covariates																			
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_041	4.3e-06 ***	0.00094 ***	0.00024 ***							0.08196 .				0.03150 *	0.00694 **				0.00748 **		0.06643 .	
MOD_042	1.96e-06 ***	0.000777 ***	0.000227 ***	0.191803						0.084743 .				0.031654 *	0.007340 **				0.007648 **		0.068265 .	
MOD_043	6.13e-06 ***	0.001353 **	0.000239 ***							0.027896 *				0.028501 *	0.008901 **			0.188074	0.008694 **		0.076037 .	
MOD_044	7.27e-06 ***	0.000722 ***	0.000163 ***											0.020749 *					0.004243 **	0.004859 **	0.042626 *	0.252587
MOD_045	8.01e-06 ***	0.001562 **	0.000187 ***								0.321176			0.022301 *					0.005927 **	0.007689 **	0.037992 *	
MOD_046	3.44e-06 ***	0.001294 **	0.000185 ***							0.078238 .				0.022830 *	0.020287 *		0.258753		0.016820 *		0.077657 .	
MOD_047	2.57e-06 ***	0.000828 ***	0.000242 ***							0.094463 .				0.029131 *	0.007243 **				0.006561 **		0.065187 .	0.372615
MOD_048	1.11e-05 ***	0.001787 **	0.000166 ***					0.489945						0.024139 *					0.005506 **	0.005831 **	0.048574 *	
MOD_049	3.87e-06 ***	0.001271 **	0.000264 ***				0.373380			0.074124 .				0.029431 *	0.005391 **				0.007658 **		0.070969 .	
MOD_050	1.63e-05 ***	0.000838 ***	0.000230 ***			0.457617								0.024625 *					0.005192 **	0.005848 **	0.057362 .	
MOD_051	1.26e-05 ***	0.001849 **	0.000169 ***						0.586866					0.025375 *					0.005189 **	0.005936 **	0.052347 .	
MOD_052	1.22e-05 ***	0.002094 **	0.000184 ***				0.568758							0.021714 *					0.004733 **	0.005270 **	0.057355 .	
MOD_053	1.89e-05 ***	0.002195 **	0.000178 ***											0.025728 *				0.768214	0.004921 **	0.006149 **	0.054696 .	
MOD_054	1.46e-05 ***	0.000894 ***	0.000171 ***	0.145908										0.143721	0.034406 *		0.064898 .			0.013223 *	0.081758 .	
MOD_055	3.63e-06 ***	0.000914 ***	0.000243 ***							0.155561	0.591456			0.030993 *	0.006994 **				0.007675 **		0.064662 .	
MOD_056	1.7e-05 ***	0.000825 ***	0.000181 ***									0.698496		0.024033 *					0.005060 **	0.011114 *	0.047637 *	
MOD_057	5.19e-06 ***	0.000846 ***	0.000247 ***							0.094710 .			0.643499	0.030593 *	0.006242 **				0.008795 **		0.065195 .	
MOD_058	1.38e-05 ***	0.001722 **	0.000177 ***										0.868815	0.022584 *					0.005513 **	0.006766 **	0.055496 .	
MOD_059	5.3e-06 ***	0.000968 ***	0.000284 ***			0.621061				0.119626				0.034757 *	0.008760 **				0.007500 **		0.073093 .	
MOD_060	1.28e-05 ***	0.001834 **	0.000176 ***											0.022752 *		0.981581			0.006738 **	0.010859 *	0.059051 .	
MOD_061	4.58e-06 ***	0.000963 ***	0.000240 ***							0.199057				0.031095 *	0.012839 *	0.821953			0.008841 **		0.065546 .	
MOD_062	4.89e-06 ***	0.000934 ***	0.000245 ***							0.092970 .		0.808590		0.033647 *	0.007244 **				0.007657 **		0.070400 .	
MOD_063	4.24e-06 ***	0.000938 ***	0.000249 ***					0.819274		0.112829				0.033903 *	0.006813 **				0.007626 **		0.067660 .	

Model_ID	Covariates																				
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_064	4.34e-06 ***	0.000968 ***	0.000240 ***						0.985662	0.105106				0.028237 *	0.007053 **				0.007483 **		0.066412 .	
MOD_065	9.7e-06 ***	0.001654 **	0.000295 ***	0.202261						0.003690 **				0.342542	0.038151 *			0.195119		0.015385 *	0.063814 .	
MOD_066	6.45e-06 ***	0.000477 ***	0.000292 ***	0.186850						0.016484 *				0.277232	0.028091 *					0.014368 *	0.047456 *	
MOD_067	8.22e-06 ***	0.0019 **	9.83e-05 ***	0.0544 .						0.0160 *					0.1095		0.0652 .			0.0102 *	0.0330 *	
MOD_068	3.73e-05 ***	0.001108 **	0.000164 ***											0.155011	0.035575 *		0.092201 .			0.012359 *	0.082967 .	
MOD_069	5.8e-06 ***	0.000617 ***	0.000305 ***	0.191804			0.312626			0.013870 *				0.258557	0.019305 *					0.012671 *	0.051614 .	
MOD_070	4.22e-06 ***	0.000418 ***	0.000280 ***	0.190995						0.020363 *				0.274184	0.029744 *					0.013235 *	0.047758 *	0.436347
MOD_071	7.11e-06 ***	0.000428 ***	0.000284 ***	0.185455						0.139163				0.258195	0.023803 *	0.464410				0.014426 *	0.045160 *	
MOD_072	7.54e-06 ***	0.000408 ***	0.000296 ***	0.188644						0.022550 *			0.492229	0.252843	0.024813 *					0.015179 *	0.045352 *	
MOD_073	6.24e-06 ***	0.001759 **	0.000101 ***	0.050104 .						0.047783 *	0.423827				0.106683		0.084598 .			0.010203 *	0.031337 *	
MOD_074	8.48e-06 ***	0.00275 **	7.98e-05 ***	0.05849 .						0.02687 *					0.04951 *		0.12493		0.34598	0.00979 **	0.03506 *	
MOD_075	5.32e-06 ***	0.000438 ***	0.000301 ***	0.178443						0.046367 *	0.531956			0.272212	0.026417 *					0.014739 *	0.045920 *	
MOD_076	7.84e-06 ***	0.002232 **	0.000111 ***	0.054828 .			0.424411			0.014080 *					0.092704 .		0.071315 .			0.009352 **	0.033700 *	
MOD_077	4.08e-06 ***	0.002209 **	0.000112 ***	0.037883 *						0.001168 **					0.000321 ***		0.069483 .	0.064137 .		0.011391 *	0.037384 *	
MOD_078	6.69e-06 ***	0.000502 ***	0.000303 ***	0.180022						0.018186 *		0.797287		0.280939	0.027041 *					0.014692 *	0.051128 .	
MOD_079	6.44e-06 ***	0.00180 **	9.57e-05 ***	0.05465 .						0.01847 *					0.06005 .		0.07040 .			0.00969 **	0.03208 *	0.56238
MOD_080	6.13e-06 ***	0.000462 ***	0.000305 ***	0.187070				0.685858		0.025209 *				0.284299	0.026950 *					0.013863 *	0.048528 *	
MOD_081	7.7e-06 ***	0.000487 ***	0.000334 ***	0.188278		0.705338				0.027335 *				0.274458	0.027236 *					0.015173 *	0.051282 .	
MOD_082	8.08e-06 ***	0.00203 **	0.00010 ***	0.05169 .						0.01792 *		0.75278			0.10799		0.06367 .			0.01063 *	0.03558 *	
MOD_083	6.3e-06 ***	0.000482 ***	0.000294 ***	0.186047					0.878735	0.021659 *				0.278398	0.027269 *					0.014202 *	0.047423 *	
MOD_084	5.06e-06 ***	0.000970 ***	0.000186 ***	0.124357						0.040019 *				0.211392	0.056803 .		0.043996 *				0.062161 .	
MOD_085	8.83e-06 ***	0.0018 **	9.72e-05 ***	0.0529 .						0.0197 *			0.6465		0.1019		0.0615 .			0.0106 *	0.0314 *	
MOD_086	9.41e-06 ***	0.001917 **	0.000121 ***	0.055430 .		0.644941				0.028337 *					0.106494		0.067134 .			0.010873 *	0.035194 *	

Model_ID	Covariates																				
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_087	7.88e-06 ***	0.001860 **	0.000102 ***	0.053359 .				0.717308		0.025369 *					0.105043		0.064080 .			0.009951 **	0.033482 *	
MOD_088	8.66e-06 ***	0.00189 **	9.55e-05 ***	0.05490 .						0.07739 .					0.11694	0.74474	0.06406 .			0.01043 *	0.03194 *	
MOD_089	1.13e-05 ***	0.001897 **	0.000121 ***	0.074822 .						0.039197 *					0.060044 .				0.145162	0.013346 *	0.038414 *	
MOD_090	8.10e-06 ***	0.00191 **	9.98e-05 ***	0.05392 .					0.86083	0.02031 *					0.10843		0.06505 .			0.01009 *	0.03295 *	
MOD_091	1.21e-05 ***	0.001057 **	0.000186 ***	0.072916 .						0.012216 *					0.086119 .					0.015544 *	0.037096 *	
MOD_092	5.51e-06 ***	0.002191 **	0.000208 ***	0.064692 .						0.001021 **					0.001651 **			0.147911		0.016805 *	0.048377 *	
MOD_093	2.14e-05 ***	0.000885 ***	8.86e-05 ***	0.049985 *											0.028589 *	0.101660	0.108442			0.012802 *	0.043697 *	
MOD_094	1.14e-05 ***	0.001306 **	0.000201 ***	0.073030 .			0.376765			0.010308 *					0.072787 .					0.013866 *	0.038373 *	
MOD_095	1.34e-05 ***	0.001077 **	0.000112 ***	0.040703 *							0.125413				0.063747 .		0.042674 *			0.013013 *	0.048718 *	
MOD_096	1.19e-05 ***	0.001367 **	0.000548 ***	0.073021 .	0.443128					0.009436 **					0.077515 .					0.016307 *	0.035524 *	
MOD_097	7.51e-05 ***	0.000414 ***	0.000271 ***											0.179079	0.056291 .					0.018407 *	0.091287 .	
MOD_098	7.68e-06 ***	0.001756 **	0.000204 ***							0.167100				0.037244 *					0.017399 *		0.041555 *	
MOD_099	8.7e-06 ***	0.000982 ***	0.000180 ***	0.074073 .						0.014889 *					0.040524 *					0.014373 *	0.035350 *	0.501052
MOD_100	3.49e-05 ***	0.000322 ***	0.000278 ***	0.202381										0.253790	0.051631 .					0.019118 *	0.096529 .	
MOD_101	1.01e-05 ***	0.000989 ***	0.000191 ***	0.069348 .						0.037170 *	0.527996				0.083632 .					0.015858 *	0.035760 *	
MOD_102	7.13e-06 ***	0.000820 ***	0.000182 ***	0.197698										0.032243 *					0.007578 **		0.072019 .	
MOD_103	1.22e-05 ***	0.001092 **	0.000193 ***	0.069599 .						0.013921 *		0.796561			0.084555 .					0.016374 *	0.039791 *	
MOD_104	1.38e-05 ***	0.001050 **	0.000227 ***	0.073335 .		0.616826				0.021622 *					0.085229 .					0.016533 *	0.039682 *	
MOD_105	3.03e-05 ***	0.001290 **	0.000105 ***	0.045757 *											0.115698		0.121383			0.014230 *	0.061140 .	
MOD_106	9.61e-06 ***	0.001746 **	0.000286 ***	0.206215						0.005369 **				0.360997	0.024428 *			0.202430			0.081117 .	
MOD_107	1.3e-05 ***	0.000998 ***	0.000189 ***	0.070891 .						0.014445 *			0.724593		0.081566 .					0.016127 *	0.035588 *	
MOD_108	1.17e-05 ***	0.001047 **	0.000196 ***	0.071216 .				0.757761		0.025168 *					0.083360 .					0.015204 *	0.037363 *	
MOD_109	1.26e-05 ***	0.001035 **	0.000182 ***	0.072614 .						0.084128 .					0.106619	0.722774				0.015679 *	0.036693 *	

Model_ID	Covariates																				
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_110	1.2e-05 ***	0.001079 **	0.000188 ***	0.072365 .					0.897324	0.017818 *					0.085576 .					0.015412 *	0.036981 *	
MOD_111	3.73e-05 ***	0.001385 **	0.000109 ***	0.058141 .											0.077270 .				0.054555 .	0.015771 *	0.068591 .	
MOD_112	2.84e-05 ***	0.00196 **	7.60e-05 ***	0.05137 .											0.05848 .		0.34346		0.19088	0.01277 *	0.06308 .	
MOD_113	1.88e-05 ***	0.001164 **	0.000121 ***	0.055562 .							0.190564				0.031862 *				0.068583 .	0.015450 *	0.056223 .	
MOD_114	8.43e-06 ***	0.000928 ***	0.000187 ***											0.029117 *					0.007451 **		0.060067 .	0.312943
MOD_115	8.26e-06 ***	0.00093 ***	0.00020 ***								0.34098			0.03589 *					0.01013 *		0.06227 .	
MOD_116	2.62e-05 ***	0.000917 ***	0.000107 ***	0.062935 .											0.015636 *	0.203233			0.118879	0.015113 *	0.051897 .	
MOD_117	1.27e-05 ***	0.001042 **	0.000203 ***											0.030189 *			0.287891		0.005687 **		0.072952 .	
MOD_118	2.62e-05 ***	0.00141 **	9.34e-05 ***	0.04935 *				0.49021							0.07690 .		0.06597 .			0.01417 *	0.05110 .	
MOD_119	3.06e-05 ***	0.001214 **	0.000157 ***	0.047743 *		0.323943									0.063927 .		0.127684			0.015373 *	0.066264 .	
MOD_120	4.22e-05 ***	0.000452 ***	0.000833 ***	0.217961	0.381257									0.237336	0.044790 *					0.019794 *	0.099912 .	
MOD_121	1.29e-05 ***	0.00104 **	0.00018 ***					0.46504						0.02890 *					0.00932 **		0.05299 .	
MOD_122	1.69e-05 ***	0.00102 **	0.00025 ***			0.42948								0.03367 *					0.00889 **		0.07539 .	
MOD_123	6.15e-06 ***	0.000797 ***	0.000990 ***	0.203397	0.309509					0.020234 *				0.315714	0.011955 *						0.062056 .	
MOD_124	3.04e-05 ***	0.00169 **	0.00031 ***	0.04724 *	0.41620										0.09865 .		0.03933 *			0.01489 *	0.06175 .	
MOD_125	2.11e-05 ***	0.002917 **	0.000196 ***											0.034998 *				0.696349	0.008551 **		0.077415 .	
MOD_126	3.75e-05 ***	0.001300 **	0.000162 ***	0.060106 .		0.313907									0.035044 *				0.054650 .	0.017073 *	0.071327 .	
MOD_127	2.08e-05 ***	0.001193 **	0.000104 ***	0.046410 *											0.116165		0.054437 .			0.012902 *	0.057874 .	0.454612
MOD_128	1.5e-05 ***	0.001060 **	0.000184 ***						0.538089					0.030026 *					0.008902 **		0.057425 .	
MOD_129	3.24e-05 ***	0.001194 **	0.000104 ***	0.043768 *									0.467945		0.058612 .		0.113024			0.014693 *	0.056598 .	
MOD_130	2.22e-05 ***	0.001271 **	0.000109 ***	0.060333 .											0.076334 .				0.053454 .	0.013878 *	0.065917 .	0.371920
MOD_131	1.8e-05 ***	0.001017 **	0.000199 ***									0.585913		0.032929 *					0.008783 **		0.067156 .	
MOD_132	5.11e-06 ***	0.000735 ***	0.000310 ***	0.191432			0.380624			0.020325 *				0.283382	0.011548 *						0.064475 .	

Model_ID	Covariates																				
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_133	3.5e-05 ***	0.003188 **	0.000104 ***	0.042322 *											0.147607		0.076817 .	0.571522		0.014079 *	0.067470 .	
MOD_134	3.16e-05 ***	0.001244 **	0.000106 ***	0.044656 *								0.579587			0.114834		0.047106 *			0.015696 *	0.068100 .	
MOD_135	3.26e-05 ***	0.00142 **	9.87e-05 ***	0.04810 *					0.54592						0.07187 .		0.05752 .			0.01466 *	0.05726 .	
MOD_136	2.96e-05 ***	0.001440 **	0.000119 ***	0.045927 *			0.508557								0.100148		0.050523 .			0.013346 *	0.062571 .	
MOD_137	6.53e-06 ***	0.000458 ***	0.000292 ***	0.187133						0.031740 *			0.446268	0.284542	0.012901 *						0.057648 .	
MOD_138	1.47e-05 ***	0.001216 **	0.000205 ***				0.662971							0.034993 *					0.008028 **		0.074110 .	
MOD_139	1.81e-05 ***	0.001263 **	0.000434 ***		0.674190									0.038920 *					0.009887 **		0.062294 .	
MOD_140	3.27e-05 ***	0.001400 **	0.000102 ***	0.066382 .				0.450847							0.040188 *				0.077652 .	0.016115 *	0.059699 .	
MOD_141	6.11e-06 ***	0.000488 ***	0.000281 ***	0.183673						0.163583				0.291954	0.013434 *	0.462450					0.058713 .	
MOD_142	1.67e-05 ***	0.001018 **	0.000193 ***										0.817493	0.035821 *					0.009425 **		0.060930 .	
MOD_143	3.95e-06 ***	0.000491 ***	0.000282 ***	0.191655						0.027476 *				0.311587	0.016161 *					0.502415	0.059803 .	
MOD_144	8.81e-06 ***	0.000980 ***	0.000401 ***	0.201620	0.708347									0.042717 *				0.008868 **			0.072040 .	
MOD_145	1.56e-05 ***	0.001133 **	0.000192 ***											0.036555 *		0.851290			0.009901 **		0.067854 .	
MOD_146	4.52e-06 ***	0.000509 ***	0.000290 ***	0.177258						0.062078 .	0.507558			0.308115	0.016261 *						0.060756 .	
MOD_147	3.59e-05 ***	0.001571 **	0.000122 ***	0.057218 .			0.508083								0.069304 .				0.056006 .	0.014565 *	0.070321 .	
MOD_148	3.93e-05 ***	0.001321 **	0.000113 ***	0.056936 .								0.533882			0.077517 .				0.055466 .	0.017519 *	0.074929 .	
MOD_149	6.14e-06 ***	0.000555 ***	0.000295 ***	0.178171						0.027398 *		0.839074		0.319990	0.015906 *						0.068131 .	
MOD_150	6.78e-06 ***	0.000560 ***	0.000334 ***	0.186786		0.622799				0.039113 *				0.307482	0.014480 *						0.067224 .	
MOD_151	3.85e-05 ***	0.001437 **	0.000105 ***	0.063454 .					0.598450						0.080375 .				0.065641 .	0.016398 *	0.065378 .	
MOD_152	4.02e-05 ***	0.001672 **	0.000254 ***	0.056765 .	0.621687										0.071508 .				0.053792 .	0.016047 *	0.068697 .	
MOD_153	3.43e-05 ***	0.003525 **	0.000111 ***	0.057507 .											0.086837 .			0.818696	0.053409 .	0.015944 *	0.072601 .	
MOD_154	5.44e-06 ***	0.000548 ***	0.000297 ***	0.186254				0.759249		0.038454 *				0.319555	0.015605 *						0.063505 .	
MOD_155	6.52e-06 ***	0.002919 **	0.000373 ***	0.057323 .	0.326024					0.020804 *					0.066829 .		0.087483 .				0.042706 *	

Model_ID	Covariates																				
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_156	3.97e-05 ***	0.001328 **	0.000115 ***	0.056502 .									0.747083		0.073775 .				0.061738 .	0.016314 *	0.066337 .	
MOD_157	5.63e-06 ***	0.000572 ***	0.000285 ***	0.186023					0.998736	0.033563 *				0.313958	0.014820 *						0.059523 .	
MOD_158	3.18e-05 ***	0.000560 ***	0.000514 ***	0.061263 .	0.455800										0.015654 *	0.053981 .				0.018990 *	0.049052 *	
MOD_159	3.3e-05 ***	0.000632 ***	0.000645 ***	0.232540	0.466235									0.081768 .					0.010466 *		0.068146 .	
MOD_160	9.76e-06 ***	0.001393 **	0.000577 ***	0.072682 .	0.411524					0.012586 *					0.055143 .						0.043095 *	
MOD_161	8.84e-06 ***	0.002462 **	0.000407 ***	0.072426 .	0.412826					0.036786 *					0.038799 *				0.171710		0.045669 *	
MOD_162	2.61e-05 ***	0.000710 ***	0.000471 ***	0.053539 .	0.658100						0.136824				0.108820					0.020126 *	0.060232 .	
MOD_163	4.13e-05 ***	0.001107 **	0.000467 ***	0.067116 .	0.437270			0.461898							0.069839 .					0.021434 *	0.057953 .	
MOD_164	5.63e-05 ***	0.000870 ***	0.000451 ***	0.056148 .	0.653378										0.123729					0.020851 *	0.075733 .	
MOD_165	1.4e-05 ***	0.001904 **	0.000453 ***	0.078117 .	0.683445					0.006143 **					0.088400 .			0.434986			0.054116 .	
MOD_166	3.25e-05 ***	0.00050 ***	0.00083 ***	0.21030	0.36266									0.26906	0.02418 *						0.11755	
MOD_167	9.13e-06 ***	0.001721 **	0.000589 ***	0.072909 .	0.437889		0.487450			0.011301 *					0.048325 *						0.044740 *	
MOD_168	8.18e-06 ***	0.001315 **	0.000566 ***	0.069346 .	0.434968					0.037567 *	0.543112				0.053513 .						0.041610 *	
MOD_169	5.52e-05 ***	0.00076 ***	0.00053 ***	0.05741 .	0.79005	0.34780									0.12032					0.02267 *	0.07642 .	
MOD_170	3.5e-05 ***	0.000767 ***	0.000427 ***	0.058287 .	0.698969										0.124034					0.018525 *	0.070341 .	0.400318
MOD_171	8.12e-06 ***	0.001291 **	0.000559 ***	0.074300 .	0.434911					0.014730 *					0.055892 .						0.041756 *	0.624724
MOD_172	5.81e-05 ***	0.00103 **	0.00047 ***	0.06226 .	0.54327				0.39295						0.12313					0.02219 *	0.06934 .	
MOD_173	1e-05 ***	0.00138 **	0.00057 ***	0.06956 .	0.47642					0.01535 *		0.84123			0.05534 .						0.04611 *	
MOD_174	1.08e-05 ***	0.001330 **	0.000607 ***	0.072782 .	0.476562	0.661019				0.023097 *					0.055123 .						0.046094 *	
MOD_175	1.01e-05 ***	0.001329 **	0.000598 ***	0.071745 .	0.389548					0.093548 .					0.066526 .	0.645314					0.040923 *	
MOD_176	1.02e-05 ***	0.001332 **	0.000562 ***	0.070758 .	0.448172					0.015053 *			0.774339		0.053041 .						0.043593 *	
MOD_177	1.02e-05 ***	0.001491 **	0.000581 ***	0.073686 .	0.407987				0.918523	0.022352 *					0.055900 .						0.043200 *	
MOD_178	9.94e-06 ***	0.001478 **	0.000577 ***	0.072577 .	0.427725			0.946324		0.036167 *					0.055742 .						0.043200 *	

Model_ID	Covariates																				
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_179	1.23e-05 ***	0.001175 **	0.000582 ***	0.202779	0.326603									0.050591 .		0.063146 .					0.078622 .	
MOD_180	2.27e-05 ***	0.001757 **	0.000337 ***	0.047071 *	0.391852										0.038684 *		0.058553 .				0.077069 .	
MOD_181	5.35e-05 ***	0.000978 ***	0.000455 ***	0.055754 .	0.696404		0.507683								0.109588					0.019398 *	0.077919 .	
MOD_182	5.82e-05 ***	0.000797 ***	0.000430 ***	0.053595 .	0.720558								0.585152		0.111539					0.021422 *	0.071136 .	
MOD_183	5.72e-05 ***	0.000802 ***	0.000415 ***	0.054644 .	0.765345							0.629975			0.125807					0.022530 *	0.081715 .	
MOD_184	8.41e-06 ***	0.001433 **	0.000698 ***	0.226746	0.417003					0.050076 .				0.121290							0.045305 *	
MOD_185	4.24e-05 ***	0.001982 **	0.000531 ***	0.056044 .	0.607490										0.126350			0.729012		0.021027 *	0.070915 .	
MOD_186	2.93e-05 ***	0.001699 **	0.000268 ***	0.055318 .	0.599916										0.053014 .				0.068547 .		0.082636 .	
MOD_187	2.35e-05 ***	0.000564 ***	0.000534 ***	0.059131 .	0.427717										0.010563 *	0.060596 .					0.057752 .	
MOD_188	6.46e-05 ***	0.002369 **	0.000251 ***											0.090405 .				0.485321			0.094959 .	
MOD_189	1.97e-05 ***	0.000744 ***	0.000462 ***	0.052917 .	0.628440						0.142613				0.039152 *						0.069441 .	
MOD_190	2.99e-05 ***	0.001143 **	0.000472 ***	0.066923 .	0.410537			0.44222							0.087686 .						0.064497 .	
MOD_191	3.29e-05 ***	0.001906 **	0.000242 ***	0.219015										0.124180				0.471979			0.095833 .	
MOD_192	4.23e-05 ***	0.000911 ***	0.000446 ***	0.055476 .	0.623712										0.090021 .						0.083576 .	
MOD_193	2.81e-05 ***	0.000833 ***	0.000634 ***	0.231186	0.461926									0.081688 .							0.088430 .	
MOD_194	1.53e-05 ***	0.000697 ***	0.000642 ***	0.216312	0.489386						0.225107			0.091376 .							0.066402 .	
MOD_195	2.09e-05 ***	0.000883 ***	0.000661 ***	0.228649	0.364698			0.299644						0.107192							0.072806 .	
MOD_196	4.09e-05 ***	0.000785 ***	0.000526 ***	0.056656 .	0.759762	0.315158									0.046128 *						0.087497 .	
MOD_197	4.22e-05 ***	0.001058 **	0.000477 ***	0.061900 .	0.510316				0.366928						0.090084 .						0.077297 .	
MOD_198	2.65e-05 ***	0.000895 ***	0.000676 ***	0.232981	0.393105				0.403589					0.090311 .							0.081839 .	
MOD_199	2.37e-05 ***	0.000726 ***	0.000671 ***	0.230924	0.421820									0.095886 .	0.423944						0.067058 .	
MOD_200	6e-05 ***	0.002940 **	0.000688 ***		0.505956									0.078143 .				0.588718			0.089185 .	
MOD_201	1.78e-05 ***	0.000738 ***	0.000585 ***	0.238290	0.500118									0.083303 .						0.416804	0.076434 .	

Model_ID	Covariates																				
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_202	2.94e-05 ***	0.000820 ***	0.000434 ***	0.058052 .	0.660974										0.090090 .						0.082197 .	0.486166
MOD_203	4.31e-05 ***	0.000819 ***	0.000398 ***	0.053720 .	0.759925							0.498998			0.091931 .						0.094554 .	
MOD_204	3.17e-05 ***	0.002330 **	0.000651 ***	0.226826	0.537226									0.110239			0.553152				0.096329 .	
MOD_205	4.28e-05 ***	0.000826 ***	0.000425 ***	0.052154 .	0.695406								0.553243		0.079854 .						0.078116 .	
MOD_206	2.93e-05 ***	0.000771 ***	0.000681 ***	0.231776	0.567332	0.464866								0.099629 .							0.092765 .	
MOD_207	4.06e-05 ***	0.001046 **	0.000458 ***	0.055307 .	0.654797		0.583852								0.081411 .						0.085872 .	
MOD_208	3.25e-05 ***	0.002086 **	0.000515 ***	0.055470 .	0.588795										0.095891 .			0.717392			0.081373 .	
MOD_209	2.93e-05 ***	0.000782 ***	0.000599 ***	0.230563	0.518010								0.635146	0.089834 .							0.084814 .	
MOD_210	3.05e-05 ***	0.000775 ***	0.000581 ***	0.223818	0.573004							0.597125		0.099251 .							0.087809 .	
MOD_211	2.74e-05 ***	0.000929 ***	0.000639 ***	0.234417	0.473406		0.786813							0.078637 .							0.083722 .	
MOD_212	2.1e-05 ***	0.001161 **	0.000223 ***	0.036065 *	0.288127													0.002424 **			0.102276	
MOD_213	1.09e-06 ***	0.000510 ***	0.000205 ***	0.037363 *	0.291733					0.000914 ***											0.035856 *	
MOD_214	7.7e-06 ***	0.001415 **	0.000117 ***	0.026021 *	0.268612														0.017243 *		0.069889 .	
MOD_215	3.59e-06 ***	0.000186 ***	0.000147 ***	0.019127 *	0.094092 .															0.030072 *	0.077109 .	
MOD_216	3.31e-06 ***	0.000512 ***	0.000165 ***	0.033049 *	0.221700			0.053120 .													0.066909 .	
MOD_217	1.22e-06 ***	0.000219 ***	0.000141 ***	0.021622 *	0.050497 .						0.069908 .										0.067272 .	
MOD_218	3.4e-06 ***	0.000241 ***	0.000136 ***	0.021247 *	0.082393 .																0.089643 .	
MOD_219	3.89e-06 ***	0.000361 ***	0.000152 ***	0.024656 *	0.128405				0.226410												0.080444 .	
MOD_220	4.97e-06 ***	0.000301 ***	0.000146 ***	0.028991 *	0.150994												0.153942				0.103023	
MOD_221	1.91e-06 ***	0.000215 ***	0.000116 ***	0.023361 *	0.073774 .																0.076895 .	0.285026
MOD_222	3.41e-06 ***	0.000201 ***	0.000153 ***	0.022787 *	0.071613 .	0.260840															0.097389 .	
MOD_223	3.89e-06 ***	0.000213 ***	0.000113 ***	0.020329 *	0.073280 .							0.300368									0.102841	
MOD_224	4.01e-06 ***	0.000211 ***	0.000149 ***	0.023514 *	0.116227											0.492048					0.075883 .	

Model_ID	Covariates																				
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_225	4.26e-06 ***	0.000218 ***	0.000139 ***	0.022608 *	0.120212		0.408230														0.082549 .	
MOD_226	5.11e-06 ***	0.000298 ***	0.000176 ***	0.026004 *	0.126689								0.683474								0.087127 .	
MOD_227	5.3e-07 ***	0.000272 ***	0.000563 ***	0.016096 *																	0.087159 .	
MOD_228	7.22e-07 ***	0.003386 **	0.000105 ***	0.366688	0.181157									0.013903 *					0.034095 *			
MOD_229	1.26e-06 ***	0.001910 **	0.000239 ***	0.406184	0.107536									0.016400 *						0.030537 *		
MOD_230	3.01e-07 ***	0.001185 **	0.000155 ***	0.448254	0.141394									0.022227 *								0.066424 .
MOD_231	1.41e-06 ***	0.000331 ***	0.000393 ***	0.449223	0.141705								0.047311 *	0.022130 *								
MOD_232	3.82e-07 ***	0.001526 **	0.000169 ***	0.410681	0.106558					0.101609				0.029281 *								
MOD_233	2.72e-06 ***	0.000784 ***	0.000231 ***	0.426383	0.160054									0.037470 *				0.246139				
MOD_234	1.08e-06 ***	0.00191 **	0.00022 ***	0.43862	0.11296									0.42663	0.38236							
MOD_235	1.08e-06 ***	0.00191 **	0.00022 ***	0.43864	0.11301									0.01659 *								
MOD_236	6.64e-07 ***	0.001865 **	0.000193 ***	0.417901	0.080505 .			0.220630						0.025646 *								
MOD_237	7.88e-07 ***	0.00111 **	6.44e-06 ***	0.41999										0.02933 *								
MOD_238	7.16e-07 ***	0.001754 **	0.000193 ***	0.420593	0.097719 .									0.013291 *			0.267686					
MOD_239	7.72e-07 ***	0.001700 **	0.000208 ***	0.430489	0.119769						0.371001			0.018705 *								
MOD_240	1.54e-06 ***	0.001793 **	0.000182 ***	0.419472	0.191969							0.493775		0.021593 *								
MOD_241	9.15e-07 ***	0.001968 **	0.000221 ***	0.432365	0.092315 .				0.440008					0.019303 *								
MOD_242	1.54e-06 ***	0.001791 **	0.000233 ***	0.451454	0.152134	0.487260								0.020452 *								
MOD_243	1.01e-06 ***	0.001844 **	0.000215 ***	0.439836	0.108568									0.019855 *		0.714456						
MOD_244	1.08e-06 ***	0.002206 **	0.000226 ***	0.450069	0.121989		0.693138							0.018144 *								
MOD_245	1.21e-06 ***	0.000401 ***	1.07e-05 ***	0.059246 .											0.006608 **							
MOD_246	1.36e-06 ***	0.000604 ***	0.000240 ***	0.052636 .	0.206875										0.004568 **							
MOD_247	8.52e-07 ***	0.000153 ***	5.19e-05 ***	0.040169 *														2.45e-06 ***				

Model_ID	Covariates																				
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_248	8.70e-07 ***	0.000151 ***	0.000146 ***	0.041009 *	0.867695													5.26e-06 ***				
MOD_249	1.08e-07 ***	0.000234 ***	3.28e-05 ***	0.019887 *															0.000968 ***			
MOD_250	2.30e-09 ***	7.08e-05 ***	3.82e-05 ***	0.022756 *						0.000855 ***												
MOD_251	2.62e-07 ***	0.000243 ***	7.49e-05 ***	0.023086 *	0.544804														0.003173 **			
MOD_252	7.92e-09 ***	8.28e-05 ***	5.62e-05 ***	0.02731 *	0.36255					0.00218 **												
MOD_253	6.30e-09 ***	0.000143 ***	4.44e-05 ***	0.019696 *				0.005235 **														
MOD_254	2.46e-08 ***	1.07e-05 ***	0.000281 ***	0.019743 *									0.000772 ***									
MOD_255	7.51e-08 ***	9.39e-06 ***	0.000224 ***	0.024000 *	0.220351								0.001639 **									
MOD_256	2.30e-08 ***	0.000174 ***	5.98e-05 ***	0.023655 *	0.472930			0.011418 *														
MOD_257	1.75e-08 ***	2.61e-05 ***	0.000183 ***	0.023155 *													0.003553 **					
MOD_258	5.09e-08 ***	2.17e-05 ***	0.000139 ***	0.028993 *	0.476376												0.011995 *					
MOD_259	9.58e-09 ***	7.76e-06 ***	3.13e-05 ***	0.0175 *	0.1662																	0.0233 *
MOD_260	2.64e-08 ***	3.90e-05 ***	0.000171 ***	0.018848 *												0.030808 *						
MOD_261	6.01e-08 ***	1.19e-05 ***	0.000109 ***	0.022752 *	0.453807											0.099914 .						
MOD_262	1.50e-09 ***	7.54e-06 ***	0.000133 ***	0.010017 *																		0.024277 *
MOD_263	2.05e-08 ***	8.45e-06 ***	5.24e-05 ***	0.0175 *	0.2305						0.0585 .											
MOD_264	3.53e-08 ***	7.88e-06 ***	7.10e-05 ***	0.0141 *	0.1766															0.0778 .		
MOD_265	5.94e-08 ***	7.81e-06 ***	4.31e-05 ***	0.015 *	0.136							0.265										
MOD_266	4.28e-09 ***	8.93e-06 ***	0.000156 ***	0.011499 *							0.039402 *											
MOD_267	3.54e-08 ***	5.94e-05 ***	6.55e-05 ***	0.0179 *	0.2739				0.1756													
MOD_268	7.40e-09 ***	5.62e-05 ***	0.000133 ***	0.012509 *					0.105742													
MOD_269	6.46e-09 ***	8.65e-06 ***	0.000286 ***	0.008078 **																0.076690 .		
MOD_270	5.48e-08 ***	6.84e-06 ***	6.46e-05 ***	0.0172 *	0.1382	0.2552																

Model_ID	Covariates																				
	Obs_min	Area_Km2	Beaufort	Sight_TTR	Douglas	SST-MEAN	SST-STD	CHL-MEAN	CHL-STD	ZEU-MEAN	ZEU-STD	PAR-MEAN	PAR-STD	DEP-STD	SLO-MEAN	ASP-sin	ASP-cos	ASP-STD	POP-STD	Dist_200m	W_north	START_OBS
MOD_271	3.76e-08 ***	7.72e-06 ***	6.14e-05 ***	0.0167 *	0.2604		0.2645															
MOD_272	9.07e-09 ***	1.95e-05 ***	0.00014 ***	0.01151 *			0.14168															
MOD_273	1.02e-08 ***	2.10e-05 ***	0.000259 ***	0.008515 **								0.404799										
MOD_274	9.38e-09 ***	1.82e-05 ***	0.000334 ***	0.009488 **		0.376573																